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TREATISE ON ZOOLOGY

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TREATISE ON ZOOLOGY

EDITED BY

SIR RAY LANKESTER

K.C.B., M.A., LL.D., F.R.S.

HONORARY FELLOW OF EXETER COLLEGE, OXFORD; CORRESPONDENT OF THE INSTITUTE OF FRANCE; LATE DIRECTOR OF THE NATURAL HISTORY DEPARTMENTS OF THE BRITISH MUSEUM

PART VII

APPENDICULATA

THIRD FASCICLE

CRUSTACEA

BY

W. T. CALMAN, D.Sc. (St. And.)

ASSISTANT IN THE ZOOLOGICAL DEPARTMENT OF THE BRITISH MUSEUM

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Introductory.—The Crustacea form one of the Classes composing the Sub-Phylum Arthropoda, and include, besides the forms popularly recognised as Crabs, Lobsters, Crayfish, Prawns, Shrimps, Sandhoppers, Woodlice, Barnacles, and Water-fleas, a multitude of related organisms which are nameless in common speech.

The Class presents so wide a range of structural diversity that it is all but impossible to give, in a few words, a definition which shall apply to all its members. Of the great majority it may be said that they are Arthropoda of aquatic habits, breathing by gills or by the general surface of the body, having two pairs of antenniform preoral appendages, and having at least three pairs of postoral appendages acting as jaws, the three corresponding somites being coalesced with the head. But while these characters are found in the more primitive members, actual or hypothetical, of all the sub-classes and orders composing the Class, the more modified types furnish exceptions to every statement of the definition. Thus, the land-crabs and woodlice are not only completely terrestrial in their habits, but are provided with special organs for aerial respiration; the preoral appendages may be modified for locomotor or prehensile functions, or may be quite wanting; and some or all of the mouth-parts may be suppressed. The most extreme modifications are found in parasitic forms, and some of these, such as the Rhizocephala, have lost, in the adult state, almost every trace, not only of Crustacean, but even of Arthropodous structure. In these cases, however, the larval stages afford indications of affinity, while less specialised forms provide connecting links with the typical Crustacea and leave no doubt as to the natural character of the Class as a whole.

Historical.—In the *Systema Naturae* (12th edition, 1767), Linnaeus placed most of the Crustacea then known in his Class Insecta (equivalent to the sub-phylum Arthropoda as now under-

stood), where they formed, with the Arachnida, one of the divisions of the Order Aptera. Three genera were recognised, *Cancer*, *Monoculus*, and *Oniscus*. The Barnacles, however, forming the genus *Lepas*, were placed among the *Vermes testacea*, between *Chiton* and *Pholas*, and the genus *Lernaea*, comprising certain parasitic forms, was classed under *Vermes mollusca*. The adjective *crustata* or *crustacea* had been applied, more or less loosely, by the older naturalists to animals possessing a hard exoskeleton, and Brisson, in 1756, had used it as the designation of a group. Pennant, in 1777, appears to be the first post-Linnaean author to suggest the separation of a distinct class under the name Crustacea, and this step was definitely taken in Cuvier's *Leçons d'Anatomie comparée* (1800), where, however, the Isopoda still remained among the Insects. Lamarck in 1801 included the Isopoda, and Latreille made many changes in the classification, the most important being the division of the class into *Malacostraca* and *Entomostraca* (*Genera Crust. et Insect.*, 1806). This arrangement, with the further division of the *Malacostraca* into *Edriophthalma* and *Podophthalma*, proposed by Leach in 1815, has been widely adopted down to the present day.

The researches of J. C. Savigny on the structure of the mouth-parts in Insects and Crustacea (1816) laid the foundations of modern conceptions of Arthropod morphology. Among his immediate successors in this line of research, perhaps the most prominent names are those of V. Audouin and H. Milne-Edwards. The *Histoire Naturelle des Crustacés* of the last-named author (1834-1840) marks an epoch in the history of Carcinology and is still indispensable to the student. It is curious that, even at this date, Milne-Edwards did not include the Cirripedia in his survey of the Crustacea, although J. Vaughan Thompson had already in 1830 described their larval stages and recognised their Crustacean affinities. Apart from this omission, the limits of the Class adopted by Milne-Edwards differ from those now generally accepted in including the Pycnogonida, the Xiphosura, and the Trilobita. There can be little doubt that the affinities of these groups are with the Arachnida, though it is possible that the very primitive Trilobites were also phyletically related to the Crustacea.

It is impossible to summarise here the numerous changes in classification introduced since the date of Milne-Edwards' work, but it may be mentioned that the establishment of a phylogenetic basis for classification is largely due to the numerous and important works of C. Claus.

Further notes on the historical development of the subject will be given in the chapters dealing with the separate sub-classes and orders.

General Morphology.

Exoskeleton.—In the Crustacea, as in other Arthropoda, the exoskeleton of the body consists typically of a series of segments or *somites* which may be movably articulated or more or less coalesced together. In its simplest form the exoskeletal somite is a ring of chitin, connected with the adjacent rings by areas of thinner integument permitting movement in various directions, and having a pair of appendages attached to its ventral surface. This ring may be further subdivided into a dorsal *tergite* and a ventral *sternite*, and the tergite may overhang the attachment of the appendage on each side as a free plate called the *pleuron*[1] (Fig. 1).

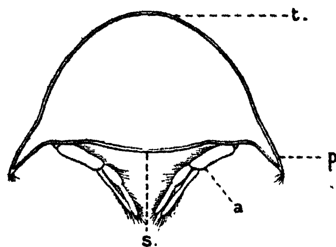


Fig. 1.

A transverse section of one of the abdominal somites of the Crayfish (*Astacus*). *a*, appendage; *p*, pleuron; *s*, sternite; *t*, tergite.

At the posterior end of the body is a terminal segment known as the *telson*, upon which the anus opens. This segment never bears typical limbs and its nature has been variously interpreted. It has been regarded as a true somite or as resulting from the coalescence of a number of somites, while some have described it as a "median appendage" or as a fused pair of appendages. Its true nature, however, is clearly shown by embryology. In the larval development of the more primitive Crustacea the body increases in length by the successive addition of new somites between the last-formed somite and the terminal region which bears the anus. The "growing-point" is, in fact, situated in front of this region, and when the full number of somites has been reached, the unsegmented part remaining forms the telson of the adult.

In no Crustacean, however, do all the somites of the body remain distinct. Coalescence of somites or suppression of segmentation (lipomerism) involves more or less extensive regions where the component somites are only indicated by the persistence of the corresponding appendages. This is constantly the case in the anterior part of the body, where a varying number of somites are united to form the head. This fusion of cephalic somites is associated with what Lankester has termed the "adaptational shifting of the oral aperture" backwards from its primitive position at the anterior end of the body. As a result of this shifting, at least two somites, corresponding to the antennules and antennae, come to lie

[1] Sometimes called the *epimeron*, but this term has been used in different senses and it seems better to abandon it altogether.

in front of the mouth in all Crustacea (Fig. 2). Perhaps an anterior somite bearing the paired eyes should also be recognised, but some doubt remains as to the appendicular nature of the eye-stalks, and it is possible that the eyes should be referred to a primitively preoral region corresponding to the prostomium of annelid worms. In any case, a prostomial element may be assumed to share in the formation of the head, and to it may be assigned the more or less problematical "frontal sense-organs" found in various larvae and some adult Crustacea. It has been suggested by Bernard that the backward shifting of the mouth was accomplished by a bending round of the anterior somites and that the prostomium is represented by the labrum or upper lip just in front of the mouth. There is, however, little definite evidence in favour of this view.

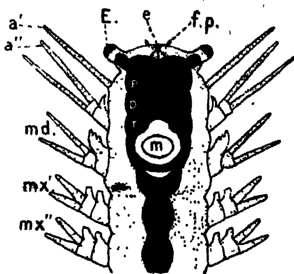


Fig. 2.

Diagram of the Crustacean head-region. (Modified from Goodrich.) The nervous system is shown in black. *a'*, antennule; *a''*, antenna; *D*, deuterocerebrum, the division of the brain corresponding to the antennules; *E*, paired compound eye; *e*, unpaired "nauplius" eye; *f.p*, frontal papilla or sense-organ; *m*, mouth; *md*, mandible; *mx'*, maxillula; *mx''*, maxilla; *P*, protocerebrum, the division of the brain corresponding to the paired eyes; *T*, tritocerebrum, the division of the brain corresponding to the antennae. Behind the mouth is seen the transverse commissure of the antennal ganglia or tritocerebrum.

In all existing Crustacea, in addition to the preoral somites, at least three postoral somites, corresponding to the mandibles, maxillulae, and maxillae, are included in the head-region. Even where a larger number of somites are involved there is generally a more or less marked change in the character of the appendages after the third postoral pair, and, since the integumental fold which forms the carapace seems to originate at this point, it is usual to take the third postoral (maxillary) somite as the limit of the cephalon throughout the Class. It is quite probable, however, that in the primitive ancestral type of the Crustacea, the head-region included a smaller number of somites. The three anterior pairs of limbs (antennules, antennae, and mandibles), which alone are present in the "nauplius" larva, show peculiarities of structure and development which seem to place them in a different category from the succeeding limbs, and there is some ground for regarding the three corresponding somites as belonging to a "primary head-region." For descriptive purposes, however, it is convenient to treat the two following somites also as cephalic.

Mention must be made here of a remarkable feature found only in the aberrant group of the Stomatopoda, among the Malacostraca. This is the reappearance of segmentation in the anterior part of the head, where two movably articulated rings carry the eye-stalks and

antennules. Whether or not these rings correspond to the primitive somites, their distinctness in the highly specialised Stomatopoda is clearly a secondary condition since it is not found in their larvae nor in any of the more primitive Malacostraca. For the same reasons no great morphological significance can be attributed to the less distinctly marked skeletal areas described as representing the ophthalmic, antennular, and antennal sternites in the higher Decapoda.

In nearly all cases the post-cephalic somites can be further grouped into regions or tagmata distinguished by the shape of the somites or the character of their appendages. In descriptive carcinology two such regions are commonly distinguished as *thorax* and *abdomen*, but it must be pointed out that there is no morphological equivalence between the tagmata so named in different groups. Throughout the Malacostraca, the thorax of eight and the abdomen of six somites are sharply distinguished by the appendages. In the other sub-classes the same names are sometimes applied to the limb-bearing and limbless regions of the trunk, while in the Branchiopoda they may denote respectively the regions in front of and behind the genital apertures.

The total number of post-cephalic somites varies within very wide limits. In the Ostracoda, where the body is not distinctly segmented, the number of trunk-limbs does not exceed two pairs. In some Branchiopoda the number of trunk-somites exceeds forty.

A structure which, from its occurrence in the most diverse groups of Crustacea, is probably a primitive attribute of the Class, is the dorsal shield or *carapace*, originating as a fold of the integument from the posterior margin of the cephalic region. In its simplest form, as seen in *Apus* among the Branchiopoda, the carapace loosely envelops more or less of the trunk. In many Branchiopoda and in the Ostracoda it forms a bivalve shell completely enclosing the body and limbs. In the Cirripedia it forms a fleshy "mantle" usually strengthened by shelly plates. In many cases among the Malacostraca the carapace coalesces with the tergites of some or all of the thoracic somites, though it may project freely at the sides, overhanging, as in the Decapoda, the branchial chambers.

It is possible that, in those cases where some of the post-cephalic somites seem to be simply fused with the head-region, a reduced shell-fold is also involved in the coalescence. This is most probably the case in the Isopoda and Amphipoda, where the fusion of the first thoracic somite with the head is clearly the last vestige of a shell-fold, traceable, with progressively diminishing extent, from the primitive Mysidacea through the Cumacea and Tanaidacea. In the Copepoda, on the other hand, in which one or two trunk-somites coalesce with the head, there is less evidence that the dorsal

"carapace" so formed really represents the shell-fold, and its lateral extensions, which cover the bases of the legs, may be the pleura of the coalesced somites. Apart from the Copepoda, the only Crustacea in which there is no trace of a shell-fold are the Anostracous Branchiopoda, and perhaps also the anomalous Malacostracan *Anaspides*.

Before proceeding to discuss the true limbs, mention must be made of certain appendages which have sometimes been regarded as homologous with the limbs, but which probably do not belong to that category. In most Malacostraca and in certain other forms, notably among the Copepoda, the posterior margin of the oral aperture is bounded by a fold forming a lower lip (*metastoma* or *hypostoma*), usually cleft into two lobes, known as the *paragnatha*, which may bear movable terminal lappets. Since there is never any corresponding pair of ganglia on the ventral nerve-chain, or other evidence of the existence of a corresponding somite, there is little ground for the view that the paragnatha are a vestigial pair of limbs. Claus has shown that in *Apus* the so-called paragnatha are probably the proximal lobes of the maxillulae, and he has suggested a similar connection in the Malacostraca, where, however, an independent origin of the lower lip seems more probable. The upper lip or *labrum*, already mentioned, is plainly an unpaired outgrowth.

The terminal segment or telson often bears a pair of processes or rami forming the "caudal furca." These may be multiarticulate filaments as in *Apus* and a few Cirripedes; in the Anostracous Branchiopoda, Copepoda, and Leptostraca they are unsegmented rods articulated to the body; in other cases they may be simple processes of the telson. There seems to be very little reason for supposing that the furcal rami represent limbs, more especially since the telson, as stated above, has not the value of a true somite.

Limbs: General Morphology.—The limbs of Crustacea differ very widely in form and structure, but it is generally possible to trace in them the modifications of a fundamental type consisting of a peduncle, the *protopodite* (or *sympodite*), bearing two rami, the *exopodite* and *endopodite*. This simple biramous form is seen, for instance, in the swimming feet of the Copepoda (Fig. 3, B), the cirri of the Cirripedia, and the abdominal appendages of the Malacostraca (Fig. 3, A), and in the second and third pairs of limbs in the earliest and most primitive type of larva, the nauplius (Fig. 3, C). As a rule, the protopodite is composed of two segments known as the *coxopodite* (or *coxa*) and *basipodite*[1] (or *basis*), but one of these may be reduced or suppressed; while, on the other hand, Hansen has shown that in some cases a pre-coxal segment can be

[1] By some writers the term basipodite is applied to the protopodite as a whole.

distinguished. The two rami may become specialised for different functions, as in the case of the thoracic limbs of Malacostraca (Fig. 3, D, E), where the endopodite forms a walking-leg, while the exopodite becomes a swimming-branch or may disappear altogether.

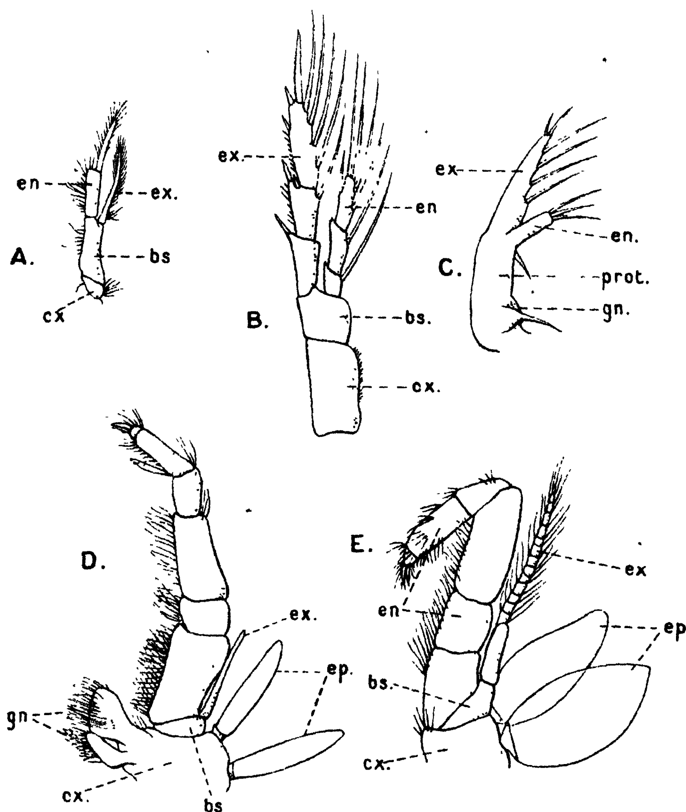


FIG. 3.

Various types of Crustacean limbs. A, abdominal limb (pleopod) of Crayfish. (After Huxley.) B, swimming-foot of *Calanus* (Copepoda). (After Sars.) C, limb of second pair (antenna) of nauplius larva of *Apus* (Branchiopoda). (After Claus.) D, first thoracic limb of *Anaspides* (Syncarida). E, second thoracic limb of *Anaspides*. *bs*, basipodite ; *cx*, coxopodite ; *en*, endopodite ; *ep*, epipodite ; *ex*, exopodite ; *gn*, gnathobase ; *prot*, protopodite.

The coxopodite often bears on the outer side an appendage (rarely more than one), known as the *epipodite*, which may function as a gill. In the appendages near the mouth one or both of the segments of the protopodite may develop, even in the nauplius, inwardly-turned masticatory processes or *gnathobases*. The occurrence of epipodites and gnathobases suggests that the primitive Crustacean limb was

more complex than the simple biramous type. Lankester has called attention to the lobed leaf-like appendages of the Branchiopoda (Fig. 4), as probably approximating to the ancestral form. As will be shown below, it is not altogether easy to recognise the homologies of the various lobes even within the limits of the group Branchiopoda, and their exact relation to the parts of the biramous limb is still open to doubt, but it is probable that the Branchiopod limb preserves characters belonging to an early phyletic stage before the biramous type had become fixed. It does not seem profitable to go beyond this and to attempt, as some have done, to compare the limbs of the Branchiopoda in detail with the Polychaete parapodium.

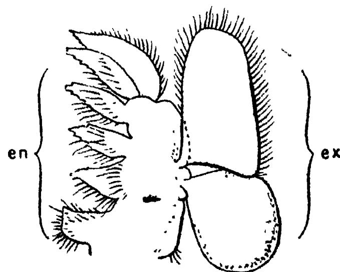


Fig. 4.

Leaf-like trunk-limb of *Lepidurus* (Branchiopoda). (After Sars.) *en*, endites; *ex*, exites.

The general character of the modifications which the original type of limb undergoes is often, though by no means always, plainly correlated with the functions which the limbs discharge. In swimming-limbs the rami are often flattened and oar-like, and fringed with plumose hairs or flattened spines. For walking or creeping one of the rami, generally the inner, is stout and cylindrical, tipped with a claw, and having the segments connected by definite hinge-joints allowing movement only in one plane. The oral appendages have the gnathobasic lobes developed at the expense of the rest of the limb, the rami persisting, if at all, only as sensory "palps." A multiarticulate flagelliform modification of the rami is generally associated with a sensory (tactile or olfactory) function, as in the antennules and antennae. A pincer-like (chelate or sub-chelate) form is frequently assumed by limbs used for prehension, the terminal segment being flexed against the penultimate, or opposed to a thumb-like process of the latter.

Special Morphology of Limbs—Ocular Peduncles.—In many Crustacea, notably in the Anostracous Branchiopoda and in the majority of the Malacostraca, the eyes are set upon peduncles which are movably articulated with the head, and which may be divided into two or three segments. The view that these peduncles are homologous with the limbs was first suggested by H. Milne-Edwards, and has been widely but not universally accepted. In spite of much discussion, however, it cannot be said that the point has been finally decided. The fact that the eye-stalks are most fully developed and most distinctly articulated not in the more primitive forms, but among the highly specialised Decapoda, is

against the appendicular theory, and the evidence of embryology does not support it. In the development of the Branchiopod *Branchipus*, Claus has shown that the eyes are, at their first appearance, sessile, and only become pedunculated at a later stage, the lateral lobes of the head on which they are set becoming produced and separated from the rest of the head by a movable articulation (Fig. 5).

The most important evidence in favour of the appendicular nature of the eye-stalks is that afforded by the phenomena of

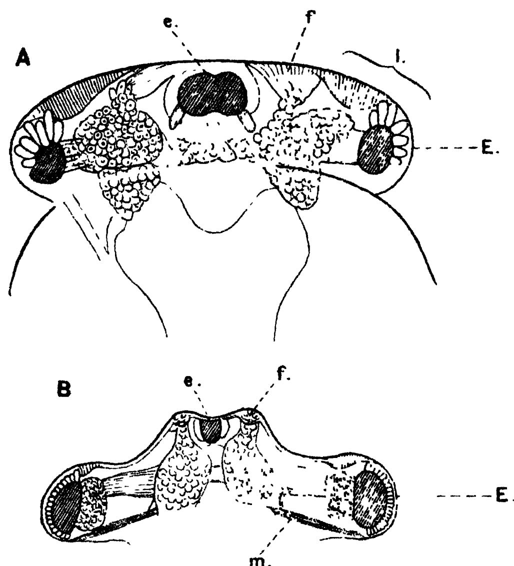


Fig. 5.

Development of ocular peduncles in *Branchipus*. (After Claus.) A, head of young larva; B, head of older larva. *l* (in A), lateral lobe of the head bearing *E*, the compound eye. In B this lobe has elongated to form the ocular peduncle, not yet movably articulated, although one of the muscles for moving it is developed (*m*). *e*, unpaired or nauplius eye; *f*, frontal sense-organs.

regeneration. If the eye-stalk be removed from a living prawn or lobster, it is found that, under certain conditions, a many-jointed appendage, like the flagellum of an antennule, may grow in its place. The bearing of such cases of "heteromorphic regeneration" on questions of homology is, however, by no means clear, and their discussion would involve a reconsideration of some of the most fundamental conceptions of current morphology. For the present it must suffice to point out that the appendicular nature of the ocular peduncles cannot be assumed as definitely proved.

The *antennules* (or first antennae) are almost universally regarded

as true appendages, although they differ from all the other appendages in the fact that they are always innervated from the brain (or supra-oesophageal ganglia), and that they are uniramous in the nauplius larva (Fig. 6, *a′*) and in the adults of all the sub-classes except the Malacostraca. As regards the innervation, an apparent exception is found in the case of *Apus*, where the antennular nerves arise, behind the brain, from the oesophageal connectives. This is undoubtedly a secondary position, however, and the nerve-fibres have been traced forward to centres in the brain. In the Malacostraca the antennules are often biramous (Fig. 7), but there is considerable doubt as to whether the two flagella correspond to the endopodite and exopodite of the other limbs. In most cases the antennules are sensory in function, but they may also be natatory or prehensile, and in the Cirripedia they form organs of attachment.

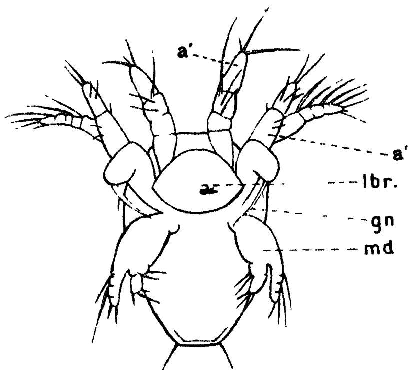


Fig. 6.
Early nauplius larva of Copepod (*Cyclops* sp.) from below. *a′*, antennule; *a″*, antenna; *gn*, gnathobasic process of antenna; *lbr*, labrum; *md*, mandible.

The *antennae* (or second antennae) are of special interest on account of the clear evidence that, although preoral in position in all adult Crustacea, they were originally postoral appendages. In the nauplius larva (Fig. 6, *a″*) their position is beside rather than in front of the mouth, and they may bear hook-like masticatory processes (*gn*) which assist the similar processes of the mandibles in seizing the food. In the Branchiopoda and less distinctly in some other groups, the nerves to the antennae arise not from the brain, but from the oesophageal connectives, and the transverse commissure of the corresponding ganglia can be traced behind the oesophagus, even in those forms in which the ganglia have moved forward into the brain (Fig. 2, p. 5).

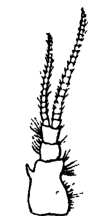


Fig. 7.
Antennule of Crayfish. (After Huxley.)

The functions of the antennae are very varied. As already stated, they act as jaws in some nauplius larvae. In many cases they are important organs of locomotion, and they may serve as sexual "claspers," or as organs of attachment in parasites. In the Malacostraca they are mainly sensory, the endopodite being a long flagellum, while the exopodite may form a flattened "scale" probably used as a balancer in swimming, or may disappear altogether.

The *mandibles*, like the antennae, are, in the nauplius, biramous swimming-limbs with a masticatory gnathobase arising from the basal segment of the protopodite. This form and function are retained with little alteration in some adult Copepoda (Fig. 8, A). In most cases, however, the exopodite is lost and the endopodite (with the distal part of the protopodite) forms the "palp" (Fig. 8, B) or may disappear altogether (Fig. 8, C), while the "body" of the mandible is formed by the coxopodite (or perhaps by the precoxa), and has a masticatory edge armed with tubercles, teeth, or spines. In parasitic forms with suctorial mouth-parts the mandibles may take the shape of piercing lancets enclosed in a tubular beak formed by apposition of the labrum and metastoma.

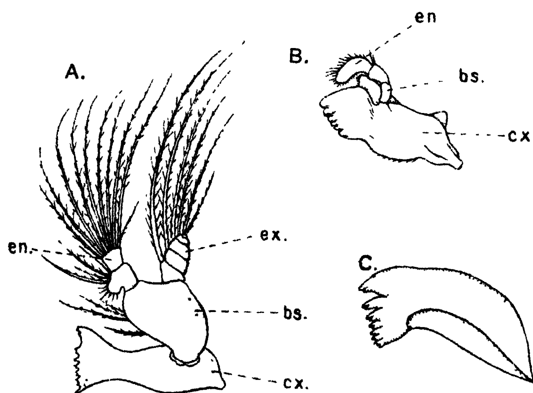


Fig. 8.

A, mandible of Copepod (*Calanus*) (after Sars); *cx*, coxopodite (or precoxa, according to Hansen), forming the "body" of the mandible; *bs*, basipodite; *en*, endopodite; *ex*, exopodite. B, mandible of Crayfish (after Huxley); letters as above. In both cases the basipodite and the segments distal to it form the "palp." C, mandible of *Lepidurus* (after Sars).

In Ostracoda the mandibular palp aids in locomotion, and in a few cases the masticatory part is greatly reduced.

The *maxillulae* and *maxillae* (or, as they are often termed, the first and second maxillae) are nearly always foliaceous appendages having gnathobasic lobes or endites borne by the segments of the protopodite (Fig. 9). The endopodite is reduced to a "palp" or is absent. On the outer side, lobes representing the exopodite and epipodite may be present. These appendages undergo great modifications in the different groups and exact comparative investigations on their morphology are still wanting.

The *post-cephalic* or *trunk appendages* vary greatly in number. In some Branchiopoda there are more than 60 pairs, while in some Ostracoda it is uncertain whether there are any. They present great diversity of form and function in the various groups

and often also in the same animal. They may be nearly all alike as in the Branchiopoda, where, at most, one or two of the anterior pairs may be specialised as sensory or as grasping organs. Commonly, as in the Copepoda, one or two of the anterior pairs are modified to assist the oral appendages and are known as *maxillipeds.* It is very characteristic of the Malacostraca that the series of trunk-limbs is differentiated into two well-defined "tagmata" or groups of similarly modified appendages, corresponding to the

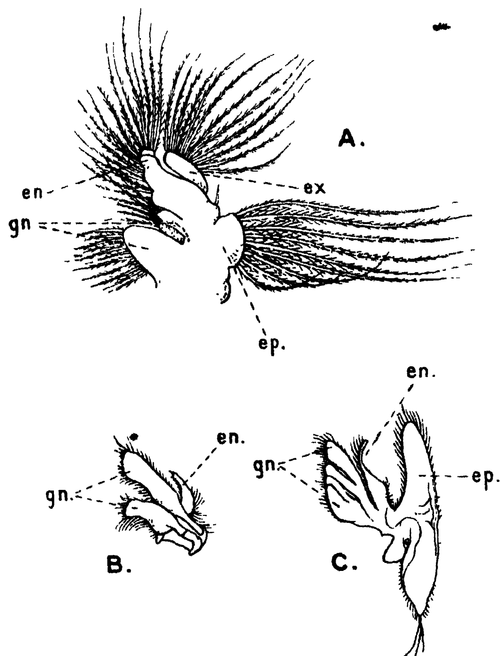


FIG. 9.

A, maxillula of Copepod (*Calanus*). (After Sars.) B, maxillula of Crayfish; C, maxilla of Crayfish. (After Huxley.) *en*, endopodite; *ep*, epipodite; *ex*, exopodite; *gn*, gnathobasic lobes. (The plate lettered *ep* in C is possibly the exopodite rather than the epipodite; see p. 268.)

thoracic and abdominal regions respectively. The thoracic limbs have the endopodites forming, as a rule, more or less efficient walking-legs, and the exopodites, when present, form swimming-branches, while the abdominal limbs are usually biramous, with the rami similar and, in the more primitive types, natatory in function. The general similarity between the appendages of each tagma is usually qualified by minor modifications, sometimes leading to the formation of subsidiary groupings. Thus, for example, in the Decapoda a group of three pairs of maxillipeds is differentiated from the thoracic tagma.

Branchiae.—In many of the smaller Crustacea there are no special branchiae, and respiration is carried on by the general surface of the body. When present, branchiae are usually formed by differentiation of parts of the appendages, often the epipodites, but the shell-fold has probably in many cases a respiratory function, and processes from its inner surface (Cirripedia) or from the surface of the body (some Ostracoda) may develop as branchiae. In the more primitive of the Malacostraca, the gills are formed by the epipodites of the thoracic limbs (*podobranchiae*), and this was probably also the original nature of those branchiae which, in the Decapoda, are attached to the articular membrane between the limb and the body (*arthrobranchiae*), or to the body-wall itself (*pleurobranchiae*). In the Isopoda the respiratory function is assumed by the lamellar rami of the abdominal appendages.

Many terrestrial Crustacea have no special adaptations for aerial respiration. In land-crabs of different families, however, the lining membrane of the branchial chamber is covered with vascular papillae and acts as a lung. Still more remarkable are the breathing organs of many of the terrestrial Isopoda or Woodlice. These are ramified tubular invaginations of the integument in the abdominal appendages, and are precisely analogous to the tracheae of other air-breathing Arthropoda.

Alimentary System.—In the great majority of Crustacea the alimentary canal is nearly straight, except at its anterior end, where it curves downwards to the ventrally placed mouth. The only cases hitherto described in which it is actually coiled upon itself are in certain Cladocera and in a single genus of Cumacea. As in other Arthropoda, it consists of *stomodaeum*, *mesenteron*, and *proctodaeum*, the first and last with a lining of chitin continuous at mouth and anus with the exoskeleton. The relative proportions of these three divisions vary greatly, and the extreme abbreviation of the mesenteron found in the common Crayfish is by no means typical of the Class. Even in the closely related Lobster this section of the gut may be several inches long.

The whole length of the alimentary canal is provided, as a rule, with circular and longitudinal muscle-fibres running in its walls, and there are often also muscle-bands extending to adjacent portions of the body-wall. In the anterior part of the stomodaeum these muscles are more strongly developed to perform the movements of deglutition. In a few Branchiopoda and Ostracoda the chitinous lining of this region develops spines and hairs which help to triturate and strain the food, and in some Ostracoda the armature assumes a more complex form as a series of toothed plates moved by special muscles. It is among the Malacostraca, however, and especially in the Decapoda, that this apparatus, the so-called "gastric mill," reaches its greatest complexity. It con-

sists of a framework of movably articulated ossicles developed as thickened and calcified portions of the lining cuticle of the "stomach" or dilated part of the stomodaeum. These ossicles bear teeth and are moved by a complex system of intrinsic and extrinsic muscles. In the posterior division of the stomach a series of pads and ridges beset with stiff hairs form a straining apparatus.

The mesenteron, in most Crustacea, has its surface increased by pouch-like or tubular outgrowths, which not only serve as glands for the secretion of the digestive juices, but may also become filled by the more fluid portion of the partially digested food and facilitate its absorption. These outgrowths vary much in their arrangement in the different groups. Most commonly there is a single pair, which may be more or less ramified, and may form a massive digestive gland ("*hepato-pancreas*" or "*liver*").

In a few parasites (Rhizocephala and the Monstrillidae among Copepoda) the alimentary canal is absent or vestigial throughout life.

Circulatory System.—The heart of the Crustacea is of the usual Arthropodous type, lying in a more or less well-defined pericardial sinus, with which it communicates by valvular openings or *ostia*. In some of the Branchiopoda, such as *Branchipus*, the heart is of the primitive tubular form, extending the whole length of the body, and having a pair of ostia in each somite. Even within the group of Branchiopoda, however, a progressive abbreviation of the heart, with a diminution in the number of ostia, can be traced, leading to the condition found in the Cladocera, where the heart is a sub-globular sac and the ostia are reduced to one pair. Among the Malacostraca, an elongated heart with numerous ostia is found only in the Leptostraca and Stomatopoda. In other cases the heart is generally abbreviated, and even where, as in the Amphipoda, it is long and tubular, the ostia are restricted in number. From the heart, the blood passes into one or more arterial trunks, which may ramify into a more or less extensive system of arterial vessels, or may open at once into the general lacunar system of the body (haemocoel). Sometimes, as in the Branchiopoda, even the arterial trunks are absent, and the blood is discharged from the anterior end of the heart directly into the lacunae of the haemocoel.

In many Crustacea, especially those of small size (many Copepoda and Ostracoda, Cirripedia), there is no heart and no definite system of vessels, and the blood is simply driven hither and thither by the movements of the body and of the alimentary canal.

Certain genera of parasitic Copepoda (*Lernanthropus*, etc.) are unique among Arthropoda in possessing a closed vascular system, containing a coloured fluid, and shut off from the general cavity of the body. The morphological relations of this system are still obscure.

Excretory System.—The most important organs of renal excretion in the Crustacea are two pairs of glands, lying at the base of the antennae and of the maxillae respectively, which are probably the survivors of a series of segmentally arranged coelomoducts present in the primitive Arthropoda. The two pairs are never fully developed at the same time in one individual, although one may replace the other in the course of development. Thus, in the Branchiopoda, the antennal gland develops early and is functional during a great part of the larval life, but it ultimately atrophies and the maxillary gland takes its place as the excretory organ of the adult. In the Decapoda, where the antennal gland alone is well developed in the adult, the maxillary gland sometimes precedes it in the larva. The structure of both glands is essentially the same (Fig. 10). There is a more or less convoluted glandular tube (*t*), of mesoblastic origin, connected internally with a closed "end-sac" (*e.s*), representing a vestigial portion of the coelom, and generally a thin-walled duct which opens to the exterior. In the Branchiopoda the maxillary gland is lodged in the thickness of the shell-fold (when this is present), and from this circumstance it often receives the somewhat misleading name of "shell-gland." In the Decapoda, the antennal gland is largely developed and often very complex, and is known as the "green gland."

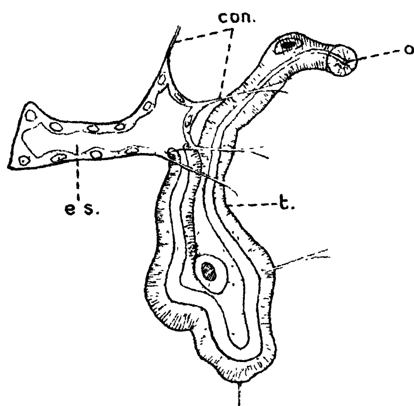


FIG. 10.

Antennal gland of a larva of *Estheria* (Branchiopoda). (After Grobben.) *con*, connective-tissue fibres; *e.s*, end-sac; *o*, external opening; *t*, glandular tubule.

Other excretory organs have been described in various Crustacea, but although their excretory functions have been demonstrated by physiological methods, their morphological relations are in most cases quite obscure. In some cases they consist of masses of mesodermal cells, within which the excretory products are stored up instead of being expelled from the body. In other cases an excretory function is attributed to certain cells of the mesenteron or to some of its diverticula.

Nervous System.—The central nervous system is constructed on the same general plan as in the other Arthropoda, consisting of a supra-oesophageal ganglionic mass or "brain," united by circum-oesophageal connectives with a double ventral chain of segmentally

arranged ganglia. In the primitive Branchiopoda the ventral chain retains the ladder-like arrangement found in some Annelids and lower worms, the two halves being widely separated and the pairs of ganglia connected together across the middle line by double transverse commissures (Fig. 11). In the other groups the two halves of the chain are approximated and more or less completely coalesced, and, in addition, a concentration of the ganglia in a longitudinal direction takes place, leading ultimately, in many cases, to the formation of an unsegmented ganglionic mass. This is seen, for example, in the Brachyura, among the Decapoda.

The brain consists, in the Branchiopoda, mainly of two pairs of ganglionic centres, the protocerebrum and deuterocerebrum (Fig. 2, P, D), giving origin, respectively, to the optic and antennular nerves. The antennal nerves arise, in this group, from ganglionic swellings on the oesophageal connectives. In the higher groups, as already mentioned, the centres for the antennal nerves have moved forwards and are included in the brain, forming the tritocerebrum (Fig. 2, T), and other additional centres are developed, so that in the highly organised Decapoda the brain assumes an extremely complicated structure.

Eyes.—Two kinds of eyes are found in Crustacea, the unpaired *median* or *nauplius eye*, and the paired *compound eyes*. The former alone is present in the nauplius larva, and it forms the sole organ of vision in the adult Eucopepoda. It may coexist with the paired eyes as in the Branchiopoda and in some of the more primitive Malacostraca, although, in the latter, it is generally vestigial. When fully developed (Fig. 12), it usually presents three divisions, each consisting of a cup-shaped mass of dark pigment (p), the cavity of which is filled with columnar retinal cells. The outer ends of these cells are continuous with the nerve-fibres (n), while at their inner ends they contain rod-like bodies (r). In some cases the three divisions of the eye are each supplied by a separate nerve

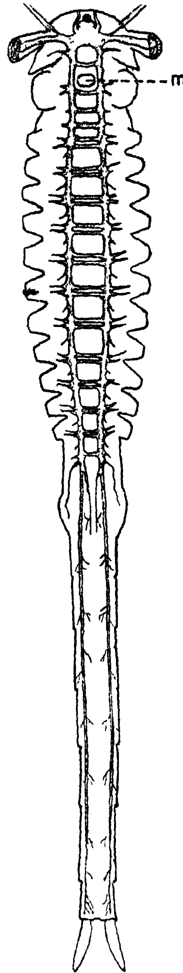


FIG. 11.

Nervous system of *Branchinecta paludosa*, one of the Branchiopoda (after Sars), showing the ladder-like form of the anterior part of the ventral nerve-chain and the absence of ganglia and of transverse commissures in the posterior limbless part of the trunk. *m* indicates the position of the mouth. The existence of a transverse commissure in front of the mouth, as shown by Prof. Sars in this drawing, is extremely doubtful. Possibly the structure observed may be a portion of the visceral nerve-ring encircling the gullet in the region of the labrum.

arising from the brain. In many cases there is no special refracting apparatus, but a refractive body, or lens (*l*), is sometimes formed on the outer side of the retinal cells, while in the Copepoda, where the median eye may undergo considerable modification, cuticular lenses and other accessory structures may be developed.

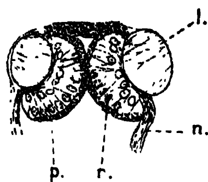


FIG. 12.

Horizontal section through the median eye of *Cypris*. (After Claus.) Only two of the three divisions of the eye are seen. *l*, lens; *n*, nerve; *p*, pigment; *r*, rod-like bodies contained in the retinal cells.

The compound eyes show considerable agreement in the details of their structure with those of Insects (Fig. 13). They consist of a varying number of *ommatidia* or visual elements, covered by a transparent region of the cuticle, the *cornea*, which is usually divided into lenticular facets. Typically each ommatidium has the structure shown in the accompanying figure. Immediately under the cuticle lie a pair of *corneagen* cells (*hy*), by which the cuticular lens is secreted and renewed on ecdysis. Below these are a group, generally two or four, of cells forming a refractive *crystalline body* (*cr*),

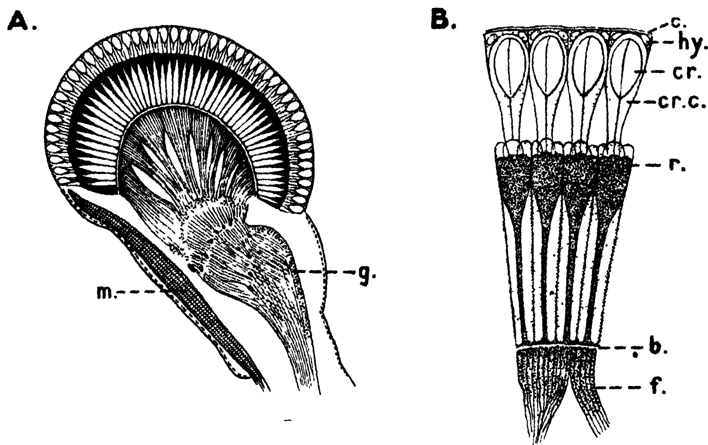


FIG. 13.

A, horizontal section of the eye and ocular peduncle of *Branchipus*. B, four ommatidia of same further enlarged. *b*, basement membrane; *c*, corneal cuticle, which in this case is not thickened to form lenses; *cr*, crystalline body; *cr.c*, cells of the crystalline body; *f*, nerve-fibrils; *g*, optic ganglia in the peduncle; *hy*, hypodermis or corneagen cells; *m*, muscle of the peduncle; *r*, retinula cells surrounding the rhabdome, which is here concealed from view by the black pigment. (After Claus.)

the lower end of which is embraced by the tips of the elongated *retinula* cells (*r*). These surround a rod-like body, the *rhabdome*, of cuticular nature but penetrated by nerve-fibrils, and usually

divisible into *rhabdomeres* corresponding in number to the retinula cells by which it is formed. At their bases the retinula cells pass into nerve-fibres (*f*) which penetrate the basement membrane (*b*) and enter the optic ganglia. Each ommatidium is more or less completely isolated by a sheath of black pigment contained partly in the retinular cells, partly in special cells lying between them. By movements in the protoplasm of these cells the position of the pigment changes according to the amount of light falling upon the eye. A layer of reflecting pigment, the *tapetum*, may also be present. It is impossible here to summarise the details of histological structure or of physiological interpretation. It may be stated, however, that the variations in structure found in different Crustacea appear to be determined not so much by the systematic affinities as by the habits of the organisms. In this connection the work of Chun and of Doflein on the structure of the eyes in pelagic and abyssal species may be referred to.

In many Crustacea, as already stated, the paired eyes are set on movable peduncles, and it is probable that this condition is the primitive one. In the primitive Branchiopoda the eyes are either pedunculated or, if sessile, movable in such a way as to suggest derivation from the pedunculate condition.

Other Sense-Organs.—The other sense-organs of the Crustacea are formed by modification of the hairs or setae on the surface of the body and limbs (Fig. 14). As in other Arthropoda, many of these setae are tactile. Each consists of a hollow conical outgrowth of the cuticle, movably articulated at the base and containing a prolongation of some of the cells of the hypodermis. One or more nerve-fibrils may be traced into the interior, and, in some cases, a ganglion-cell in connection therewith lies at the base of the seta. When feathered, or provided with secondary barbs, the setae will respond to movements or vibrations in the surrounding water, and to some setae of this type an auditory function has been attributed (Fig. 14, C). In certain Malacostraca more specialised organs are found which have been regarded as auditory. In most Decapoda there is an invagination of the integument in the basal segment of the antennule having plumose "auditory" setae on its inner surface. In some cases the sac remains open to the exterior, permitting the introduction of sand-grains which act as "otoliths." In other cases the sac is completely closed, and may then contain a single "otolith" secreted by its walls. Otocysts are found in a few other Malacostraca in various positions; for example, in the endopodites of the uropods in the Mysidae.

Recent investigations have rendered it doubtful, however, whether aquatic Crustacea can hear at all, in the proper sense of the term, and it has been shown that one function, at least, of the

so-called "otocysts" is connected with the equilibration of the body. They are more properly, therefore, termed "statocysts."

Another modification of sensory setae is believed to be associated with the sense of smell. In most Crustacea the anntenules and often also the antennae bear groups of hair-like filaments, sometimes slender, sometimes more or less swollen, in which the cuticle is extremely delicate. These are known as *olfactory filaments* or *aesthetases* (Fig. 14, A, B). They are often more strongly developed in the male sex, and are believed to guide the males in pursuit of the females.

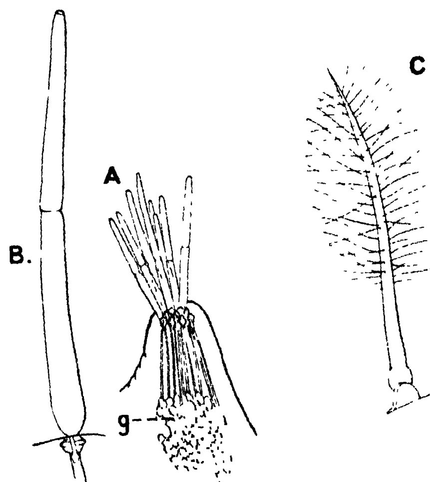


Fig. 14.

A, antenna of *Daphnia magna* bearing a group of "olfactory filaments." *g*, nerve-ganglion sending fibrils to the olfactory filaments. B, one of the filaments further enlarged. (After Scourfield.) C, "auditory" seta from peduncle of antennule of *Mysis relicta*. (After Sars.)

Glands.—Apart from the digestive and excretory glands already mentioned, and from other glandular structures to be described in connection with the reproductive system, many Crustacea possess *dermal glands* scattered over the surface of the body and limbs or grouped at certain points for the discharge of special functions. These consist of single cells or groups, traversed by ramified intra-cellular canals, and communicating with the exterior by fine ducts. Such glands occurring on the walls of the oesophagus or in the neighbourhood of the mouth have been regarded as salivary in function. Others on the surface of the body and limbs may be used, as in some Amphipoda, for the construction of tubular cases or nests in which the animals live, or, as in some Copepoda, may secrete a gelatinous envelope enabling the animals to survive dessi-

cation. Others, again, are believed to have a poisonous function. The greatly developed *cement-glands* of the Cirripedia are possibly related to the same group of structures.

Phosphorescent Organs.—In this connection may be mentioned the power of phosphorescence possessed by many Crustacea. In some cases this is due to a luminous secretion produced by certain of the dermal glands. In the Euphausiacea and certain Decapoda, however, complex and remarkable light-producing organs are present, which were formerly described as "accessory eyes."

Reproductive System.—In the great majority of Crustacea, as in other Arthropoda, the sexes are separate. Apart from certain isolated instances, possibly abnormal and probably non-functional, among Branchiopoda and Amphipoda, the only exceptions are the sessile Cirripedia and some parasitic Isopoda (Cymothoidae and Cryptoniscina), where hermaphroditism is the rule.[1] Parthenogenesis is frequent among the Branchiopoda and Ostracoda, often in more or less definite cyclical alternation with sexual reproduction. Where the sexes are distinct a more or less marked sexual dimorphism often exists. The male is frequently provided with clasping-organs for holding the female, and these may be formed by the modification of almost any of the appendages, often the antennules or antennae, or some of the trunk-limbs, or even the mandibular palp (some Ostracoda). In addition, some of the appendages in the neighbourhood of the genital apertures may be modified for the purpose of transferring the sperms to the female. In the higher Decapoda the male is generally larger than the female and has stronger chelae. In the other groups the male is often the smaller, and in many parasitic Copepoda and Isopoda this disparity in size is carried to an extreme degree, and the minute male is attached, like a parasite, to the enormously larger female. The remarkable and complex sexual relationships of the Cirripedia will be discussed in the section dealing with that group.

The gonads of the Crustacea, as of other Arthropoda, are hollow organs, the cavity communicating with the efferent ducts. They are primitively paired but often coalesce partially or completely with each other on the dorsal side of the alimentary canal. The ducts are present only as a single pair, except in certain parasitic Isopoda (Hemioniscidae, Liriopsidae), where two pairs of oviducts are found. Various accessory structures may be developed in connection with the efferent ducts in both sexes. The oviducts may have diverticula serving as *receptacula seminis* (in cases where internal impregnation takes place), and may be provided with glands secreting envelopes or shells around the eggs. Similarly the glandular walls of the *vasa deferentia* may secrete spermatophores

[1] According to recent observations (as yet unpublished) by Mr. Alf Wollebaek, certain deep-sea Decapoda also are normally hermaphrodite.

or capsules in which the sperms are transferred to the female. The terminal portion of the male duct is sometimes protrusible, and acts as an intromittent organ, or this function may be discharged by some of the appendages.

The position of the genital apertures varies greatly in the different groups. The most anterior position is found in the Cirripedia, where the oviducts open on the first trunk-somite, while in certain Branchiopoda (*Polyartemia*), on the other hand, the genital apertures lie behind the nineteenth trunk-somite. It is characteristic of the Malacostraca that the position of the genital apertures is different in the two sexes, the female openings being on the sixth and the male openings on the eighth trunk-somite. In all the other groups, with exception of the hermaphrodite Cirripedia, the position is the same in the two sexes.

While very few Crustacea are viviparous in the sense that the eggs are retained within the body until hatching takes place (some Branchiopoda), the great majority carry the eggs in some way or other after their extrusion. The various devices by which this is accomplished will be described in dealing with the different groups; but it may be mentioned here that a few cases are known (Cladocera, terrestrial Isopoda) in which the developing embryos are nourished by a special secretion while in the brood-chamber of the mother.

Embryology.

The majority of the Crustacea leave the egg in a form more or less different from that of the adult, and pass through a series of free-swimming larval stages, but there are many cases of direct development in which the newly hatched young resemble the parent in general structure. The relative size of the egg is greater in those forms which develop without metamorphosis, except where other means exist for the nourishment of the developing embryos.

The details of the early stages of development differ considerably within the limits of the class. They are chiefly of interest, however, from the point of view of general embryology rather than from that of the special student of the Crustacea, and can only be very briefly referred to here. An admirable summary of the whole subject will be found in Korschelt and Heider's *Text-book of the Embryology of Invertebrates*.

Segmentation is usually of the superficial or centrolecithal type, or some modification thereof. The hypoblast is formed either by a definite invagination or by the immigration of isolated cells which wander through the yolk as "vitellophags" and later become associated to form the mesenteron, or by some combination of the two methods. The blastopore generally occupies a position corresponding to the posterior end of the body. The mesoblast of the

cephalic (naupliar) region probably arises in connection with the lips of the blastopore and consists of mesenchymatous cells. In the region of the trunk, in many cases, paired mesoblastic bands are formed, growing in length by the division of teloblastic cells at the posterior end and becoming segmented into somites. The occurrence of true coelom-sacs is doubtful. The rudiments of the first three pairs of appendages, antennules, antennae, and mandibles, commonly appear simultaneously and, even in forms with embryonic development, they often show differences in their mode of appearance from the succeeding limbs. When this stage, corresponding to the nauplius stage of larval development, is passed through within the egg, it is often marked by the formation of a cuticular membrane within which the further development proceeds.

The complex and varied larval metamorphoses of the Crustacea have been the subject of much discussion in view of their bearing on the phylogenetic history of the group. In those Crustacea in which the series of larval stages is most complete the starting-point is the form already mentioned under the name of *nauplius*. The typical nauplius (Fig. 6, p. 11) has an oval unsegmented body and three pairs of limbs, corresponding to the antennules, antennae, and mandibles of the adult. The antennules are uniramous, the others biramous, and all three pairs are used in swimming. The antennae may have a spiniform or hooked masticatory process at the base, and share with the mandibles, which have a similar process, the function of seizing and masticating the food. The mouth is overhung by a large labrum or upper lip, and the integument of the dorsal surface of the body forms a more or less definite dorsal shield. The paired eyes are, as yet, wanting, but the median eye is large and conspicuous. A pair of papillae or filaments, probably sensory, are commonly present at the anterior end. Nauplius larvae, differing only in details from the typical form just described, are found in very diverse groups of the Crustacea, such as the Branchiopoda, Copepoda, Cirripedia, and some Malacostraca. In many forms which hatch from the egg at a more advanced stage there is, as already mentioned, more or less clear evidence of an embryonic nauplius stage. It seems certain, therefore, that the possession of a nauplius larva must be regarded as a very primitive character of the Crustacean stock.

As development proceeds, the body of the nauplius elongates and indications of segmentation begin to appear in its posterior part. At successive moults the somites increase in number by the addition of new somites, behind those already differentiated, from a formative zone in front of the telsonic region. In the most primitive cases, the appendages posterior to the mandibles make their appearance, like the somites which bear them, in regular

order from before backwards. The limb-buds early become bilobed and grow out into typically biramous appendages which gradually assume the characters found in the adult. With the elongation of the body, the dorsal shield of the nauplius begins to project posteriorly as a shell-fold, which becomes the carapace. The rudiments of the paired eyes appear under the integument of the head, but only become pedunculated at a comparatively late stage.

The course of development outlined above, leading from the nauplius to the adult form by the successive addition of somites and appendages in regular order, agrees so well with the process observed in the development of the typical Annelida, that it must be regarded as the most primitive. It is most closely followed by such Branchiopoda as *Apus* and *Branchipus*, and by some Copepoda. In the majority of Crustacea, however, this primitive scheme is more or less modified. The earlier stages may be passed through within the egg or in the maternal brood-chamber, so that the larva only begins to lead an independent existence at a stage more advanced than the nauplius. Further, the gradual appearance of the successive somites and appendages may be accelerated, so that great advances in structure take place at a single moult. For example, in the Cirripedia, the latest nauplius stage gives rise directly to the so-called *Cypris*-larva, which possesses all the appendages of the adult. Another common modification of the primitive method of development consists in the accelerated appearance of certain somites or appendages, disturbing the regular order of development. This modification is especially found in the Malacostraca, in which, even among those which have most closely adhered to the primitive order of development, the last pair of abdominal appendages usually make their appearance before those immediately in front of them. The same process, carried further, leads to the very peculiar larva known as the *zoea*, in the typical form of which, found in the Brachyura, the posterior five or six thoracic somites are greatly retarded in development, and are still represented by a short unsegmented region of the body at a stage when the abdominal somites are fully formed and even carry appendages.

A remarkable phenomenon observed in the development of a few Malacostraca is the temporary retrogression and even disappearance of certain appendages which redevelop in later stages. The best-known instances of this will be further alluded to in describing the development of the Penaeidea among the Decapoda.

In addition to the nauplius and zoëa there are many other types of Crustacean larvae distinguished by special names, though, as their occurrence is restricted within the limits of the smaller systematic divisions, they are of less general interest. We need only mention here the *metanauplius*, a vaguely defined stage following the nauplius,

possessing rudiments of some of the post-naupliar somites and appendages.

Most of the larval forms are pelagic in habit, and many show special adaptations to this mode of life, especially in the development of spines and processes which are probably less important as defensive organs than as aids to flotation.

PHYLOGENY.

The study of fossil Crustacea has hitherto contributed comparatively little towards a precise knowledge of the phylogenetic history of the class. Although their remains are abundant in nearly all formations, from the most ancient up to the most recent, in very many cases only the carapace or shell is preserved, the limbs being lost or represented only by indecipherable fragments. Many important forms must have escaped fossilisation altogether owing to their small size and delicate structure. Further, many important groups were already differentiated when the geological record began. The Branchiopoda, Ostracoda, and Cirripedia are represented in Cambrian or Silurian rocks by forms which seem to resemble those now existing, so that palaeontology can have little light to throw on the mode of origin of these groups. In the case of the Malacostraca the material is a little more promising. It is not improbable that the Phyllocarida, which are found from the Cambrian onwards, may include the forerunners of the true Malacostraca, but nothing is definitely known of their appendages. The recent discovery, in the Tasmanian *Anaspides* and the Australian *Koonunga*, of what are believed to be representatives of the Carboniferous and Permian Syncarida, has given a clue to the affinities of forms hitherto problematical, and may throw light on the relations of other Palaeozoic fossils hitherto vaguely referred to "Schizopoda" or Decapoda. Remains of undoubted Decapods are first met with in Mesozoic rocks. They are abundant in many deposits, and are sometimes sufficiently well preserved to render possible fairly accurate determination of their affinities. The Isopoda and Stomatopoda are known from Mesozoic deposits, but have hitherto yielded no results of phylogenetic importance.

In view of the scarcity of trustworthy evidence as to the actual forerunners of existing Crustacea, phylogenetic conclusions based on the data of comparative anatomy and embryology remain largely speculative. They are none the less a necessary preliminary to the attempt to construct a natural system of classification.

The earlier speculations on this subject started from the assumption that the "theory of recapitulation" could be applied to the larval history of the Crustacea. The various forms of larvae, more especially the nauplius and the zoëa, were supposed to reproduce,

more or less closely, the actual structure of ancestral types. As regards the zoëa, this assumption was soon shown to be erroneous, and the secondary nature of this type of larva is now generally admitted. The nauplius, however, by the constancy of its general characters in the most widely diverse groups, shows itself to be a very ancient type, and the view has been advocated that the Crustacea have arisen from an unsegmented nauplius-like ancestor. To this view there are considerable objections. Several structures which can hardly have been absent from the common stock of the Crustacea, such as the paired eyes and the shell-fold, are not found in the nauplius. Other characters common to certain Crustacea and Annelids, such as the mode of growth of the somites, the structure of the nervous system and of the heart, can hardly be supposed to have arisen independently in the two groups. The view now most generally adopted is that the Branchiopoda, and especially *Apus*, which resemble the Annelids in the characters just mentioned and also in the large number and uniformity of the trunk-somites and their appendages, approach most nearly to the primitive Crustacean type. On the other hand, in some respects, such as the reduced mouth-parts, the Branchiopoda are considerably specialised. In some Copepoda the cephalic appendages are much more primitive than in the Branchiopoda, and the first three pairs of appendages retain throughout life, with little modification, the shape and function which they have in the nauplius stage. It is possible, however, that in these characters the Copepoda are persistently larval rather than phylogenetically primitive, and in other respects, especially in the absence of paired eyes and of a shell-fold, they are certainly specialised.

In order to reconstruct the hypothetical ancestral type, therefore, it is necessary to combine the characters of several of the existing groups. It may be supposed to have approximated, in general form, to *Apus*, with an elongated body of numerous similar somites, terminating in a caudal furca; with the postoral appendages all similar, and with a carapace originating as a shell-fold from the maxillary region. The eyes were probably stalked and movable, the antennules uniramous, and the antennae and mandibles biramous and natatory, and both armed with masticatory processes. The trunk-limbs were probably biramous but with additional endites and exites, and all provided with gnathobases.

It is to be noted that the Trilobita, which, according to the classification adopted in this work, are dealt with under Arachnida, approximate to the structure of the primitive Crustacean here sketched except in the absence of a shell-fold and in having the eyes sessile.

It is not necessary, on this view, to deny all phylogenetic significance to the nauplius. It may be regarded as an ancestral

larval form, corresponding perhaps (as Hatschek suggests) to the stages immediately succeeding the trochophore in the development of Annelids, but with some of the later-acquired Crustacean characters superposed upon it.

The five sub-classes into which the Crustacea are divided in the classification here adopted appear to represent independent or nearly independent lines of descent from the primitive stock. Their relations to each other and the probable course of evolution within each group will be dealt with in subsequent chapters.

It may be mentioned that the classification introduced by Latreille in 1806, in which the Malacostraca are opposed to all the other Crustacea grouped together under the name of Entomostraca, is still frequently adopted. The Entomostraca, however, like the Invertebrata, constitute a very heterogeneous group, defined only by negative characters and having no claim to retention in a natural system of classification.

Literature.

(*Selection of important works dealing with the Class as a whole.*)

In this list and in those appended to the following chapters no attempt has been made to give a complete bibliography of the subject. The references given in the works mentioned will, however, provide the necessary guidance for the student who desires a further acquaintance with the vast mass of carcinological literature.

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CHAPTER II

THE BRANCHIOPODA

SUB-CLASS BRANCHIOPODA, Latreille (1817).

Order 1. **Anostraca.**
„ 2. **Notostraca.**
„ 3. **Conchostraca.**
„ 4. **Cladocera.**
Sub-Order 1. **Calyptomera.**
Tribe 1. Ctenopoda.
„ 2. Anomopoda.
Sub-Order 2. **Gymnomera.**
Tribe 1. Onychopoda.
„ 2. Haplopoda.

Definition.—Crustacea in which the carapace may form a dorsal shield or a bivalve shell or may be entirely absent; the number of trunk-somites varies greatly; the posterior part of the trunk is without limbs and usually ends in a caudal furca; the antennules are generally reduced and unsegmented; the mandibles have no palp or only a vestige of one; the maxillae are reduced or absent; the trunk-limbs, which vary greatly in number, are generally of uniform structure, rarely pediform, generally foliaceous and lobed; the position of the genital apertures varies greatly; the paired eyes are rarely absent; development usually with metamorphosis; young hatched in nauplius or metanauplius stage.

Historical.—The earliest mention of any of the Branchiopoda is found in the works of Swammerdam, who, in 1669, described a species of *Daphnia* as "Pulex aquaticus arborescens," and the name of "water-fleas" has since been commonly applied to the group of Cladocera. *Apus* and *Branchipus* were described early in the eighteenth century, and, together with *Daphnia*, formed the subjects of a series of remarkable memoirs (1752-1756) by J. C. Schäffer. The classical work of O. F. Müller, *Entomostraca seu Insecta testacea* (1785), described a large number of new types and

laid the foundations of classification. The order Branchiopoda, as first defined by Latreille in 1817, included Ostracoda, Copepoda, and *Limulus*; and Milne-Edwards, in 1840, while excluding these, retains the later added *Nebalia*. Later attempts to extend the limits of the group to readmit the Ostracoda and Branchiura have not met with support, while Claus's demonstration of the Malacostracan affinities of *Nebalia* and its allies is now generally accepted. Among the authors who, in the first half of the nineteenth century, contributed to a knowledge of the group, Jurine, Fischer, and Baird may be mentioned. Zaddach's monograph on *Apus* is still the chief source of information on many points of anatomy. Leydig's work on the Cladocera is especially important as regards internal anatomy and histology; and Weismann's series of papers deal, among many other points, with the remarkable phenomena of their reproduction, which had attracted attention from the time of Schäffer. As is the case with most other groups of Crustacea, modern conceptions of the morphology of the Branchiopoda are largely indebted to the works of Claus. Lankester's paper on the appendages and nervous system of *Apus* greatly influenced opinion in favour of the primitive position of the Branchiopoda. Among the more purely descriptive and faunistic works the numerous papers of G. O. Sars hold an important place, and mention may also be made of the fine monograph on the Cladocera of Sweden, published

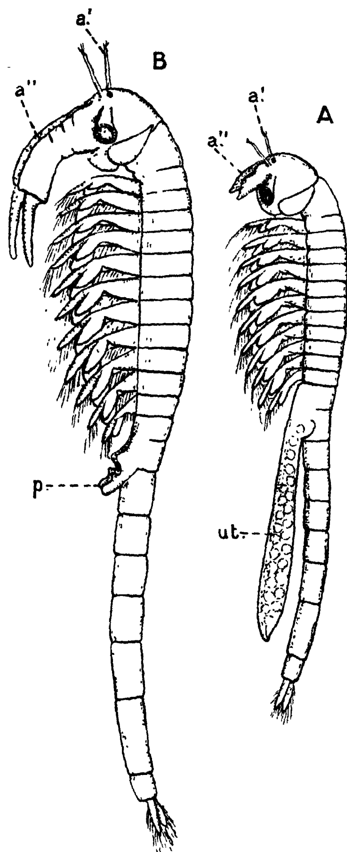


FIG. 15.

Branchinecta paludosa, one of the Anostraca. × 4. (After Sars.) A, female; B, male. *a'*, antennules; *a''*, antennae, enlarged in the male to form clasping organs; *p*, paired penes of the male; *ut*, ventral prolongation of the genital segment in the female, containing the "uterus" filled with eggs. On the front of the head, between the antennules, is the unpaired eye, and, just behind it, the stalked compound eye. Dorsal to the pear-shaped mandible is seen the groove which appears to divide the head-region into two segments. Following this, the trunk shows eleven limb-bearing and eight limbless somites (besides the telson), the first and second of the latter partly coalesced.

in 1900 by Lilljeborg, who had made important contributions to the subject so long ago as 1853.

Morphology.

The Branchiopoda present considerable diversity of general shape. In the Anostraca there is no shell-fold, and the elongated

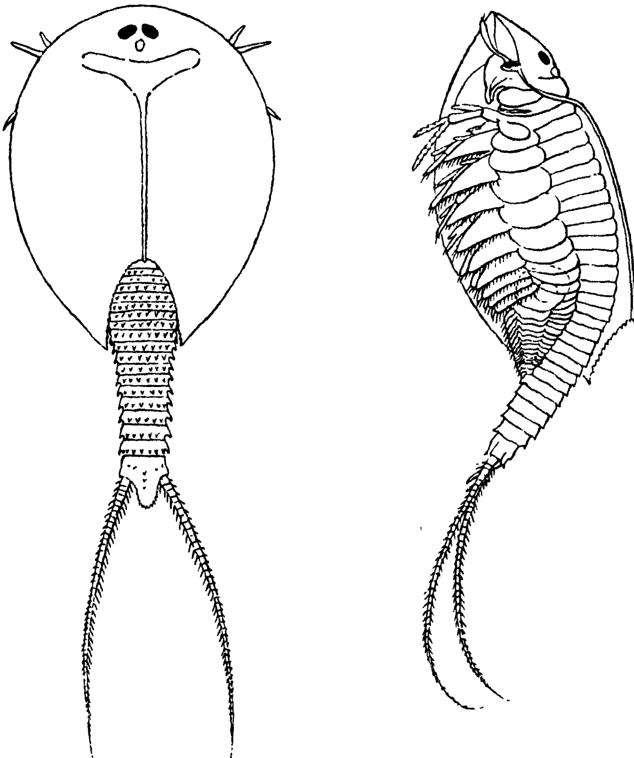


Fig. 16.

Lepidurus glacialis, one of the Notostraca. × 2½. (After Sars.) Dorsal view on the left, lateral view on the right. In the latter, one-half of the carapace has been cut away to show the segmentation of the trunk and the appendages. On the dorsal surface are seen the paired eyes with the "dorsal organ" behind and between them, the median dorsal ridge of the posterior part of the carapace, and the two transverse grooves just behind the eyes.

body, composed of many distinct somites, has an almost vermiform aspect (Fig. 15). The flattened natatory feet are more laterally placed than is usual in Crustacea, increasing the resemblance to the Chaetopod worms. In the Notostraca also the body is elongated, and composed of numerous somites, but its anterior portion is covered by a broad arched carapace (Fig. 16). In the

Conchostraca the body tends to be laterally compressed, and is completely enclosed in a bivalved shell closely simulating that of some lamellibranchiate molluscs (Fig. 17). In the Cladocera the body is composed of few somites and its segmentation is more or less obscured, while the bivalve shell, in most cases, covers the body and limbs, leaving the head free (Fig. 18).

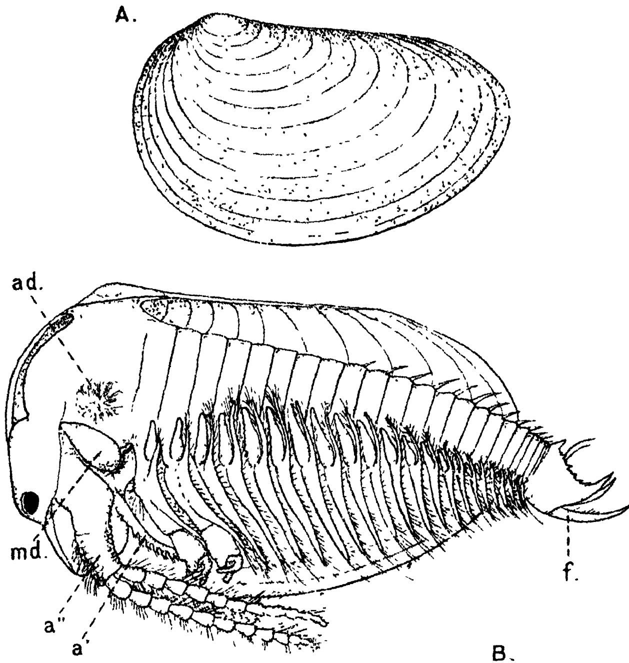


FIG. 17.

Estheria obliqua (Conchostraca). A, shell of female, from the left side. B, male seen from the side, after removal of left valve of shell. (After Sars.) *a'*, antennule; *a''*, antenna; *ad*, adductor muscle; *f*, caudal furca; *md*, mandible. On the first and second pairs of trunk-limbs are seen the "claspers" of the male.

Except in the Cladocera, the head is defined from the first trunk-somite. In the Anostraca it is divided into two portions by a transverse groove which crosses the dorsal surface just above the mandibles. This groove is also found in the Conchostraca, and it is no doubt homologous with the anterior transverse groove on the dorsal surface of the carapace in the Notostraca. In the Conchostraca and Cladocera the front of the head is more or less produced downwards forming a rostral process, and in the Notostraca it is inflected, forming a sharp semicircular anterior edge continuous on either side with the lateral margins of the carapace.

The carapace may be directly continuous in front with the dorsal integument of the head as in most Cladocera, or defined from it by a groove as in some Cladocera and the Notostraca. In the Conchostraca the connection between the animal and the shell is reduced to a comparatively narrow neck and the lateral lobes of the shell extend forwards on each side so as to enclose the whole head (Fig. 17). Generally the shell-fold does not coalesce with any of the trunk-somites which it envelops, with the exception of the one or two anterior somites which in the Cladocera are fused with the head. In the aberrant Cladoceran *Leptodora*, however, it coalesces with the dorsal surface of the leg-bearing somites, and its free portion, which here, as in some other Cladocera, forms merely a brood-sac, appears to arise from the posterior margin of the sixth trunk-somite (Fig. 19).

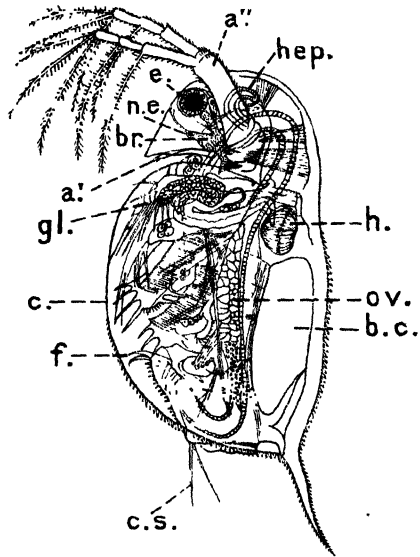


FIG. 18.

Daphnia, female. *a'*, antennule; *a''*, antenna; *b.c*, brood-chamber; *br*, brain; *c*, margin of carapace; *c.s*, caudal setae; *e*, compound eyes coalesced into one; *f*, furca; *gl*, maxillary gland; *h*, heart; *hep*, hepatic diverticulum of gut; *n.e*, nauplius eye; *ov*, ovary. (After Claus and Grobben.)

The carapace may be more or less corneous, but it is never strongly calcified. In a few Cladocera (*Monospilus*, etc.) and in the Conchostraca (Fig. 17) the integument of the outer surface of the shell is not cast off in ecdysis, but remains in position, giving rise to a series of "lines of growth" marking the increased size of the shell at each moult. Special modifications of the carapace for protection of the eggs will be referred to below.

The number of trunk-somites varies very much. It is greatest in the Notostraca, where 42 somites are found in certain species of *Apus*. In the Conchostraca the number is from about 13 to 28, and in the Anostraca 19 to 23. In the Cladocera the segmentation of the body is generally more or less obscured; at least the first two somites are always coalesced with the head. In *Daphnia*, according to Claus, these are followed by three limb-bearing somites, and the succeeding apodous region is divided in the young into three "abdominal" somites and a "postabdomen"

or telson. This segmentation of the apodous region is distinctly retained in the adult *Leptodora* (Fig. 19).

Apart from the presence or absence of appendages, the trunk of the Branchiopoda is not differentiated into distinct regions. By various authors the terms "thorax" and "abdomen" have been applied respectively, sometimes to the pre- and post-genital, sometimes to the limb-bearing and limbless regions of the trunk. As the limits between these regions do not coincide, even approximately,

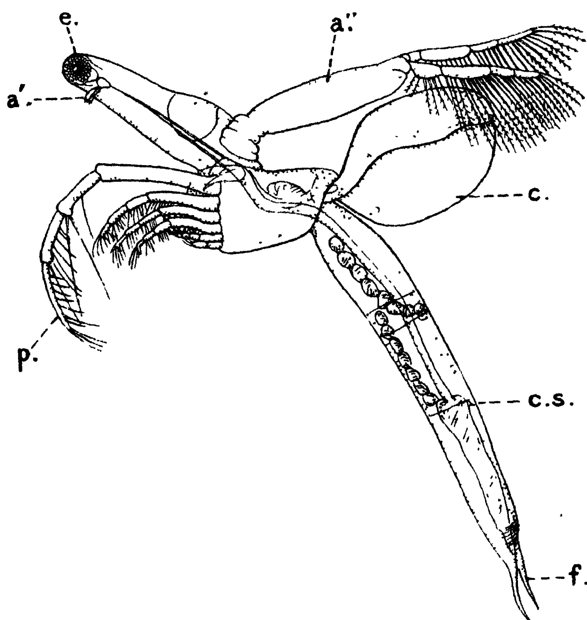


FIG. 19.

Leptodora kindtii, female, × 10. *a'*, antennule; *a''*, antenna; *c*, carapace, reduced to a brood-sac; *c.s*, caudal setae (compare figure of *Daphnia*, p. 33); *e*, compound eye; *f*, furca; *p*, first trunk-limb. (After Lilljeborg.)

except in the Anostraca, it seems better to avoid altogether the use of the terms "thoracic" and "abdominal" in dealing with this group.

In the Notostraca a varying number (4-14) of the posterior somites are without appendages. In the post-genital region of the body the number of pairs of appendages greatly exceeds the number of somites, some of the posterior somites carrying as many as six pairs. In the Anostraca there are from four to nine limbless somites, but at least the two anterior are coalesced to form the genital segment. In the Conchostraca the short post-pedal region is unsegmented.

The last segment of the body, or telson, carries, except in *Limnetis* and *Thamnocephalus*, a pair of furcal rami, long antenniform filaments in the Notostraca (Fig. 16), unsegmented styles or flattened plates in the Anostraca (Fig. 20, C). In the Conchostraca and Cladocera the posterior part of the body is flexed ventrally and the furca is represented by a pair of strong curved claws (Fig. 17, *f*). The anus opens either at the end of the body

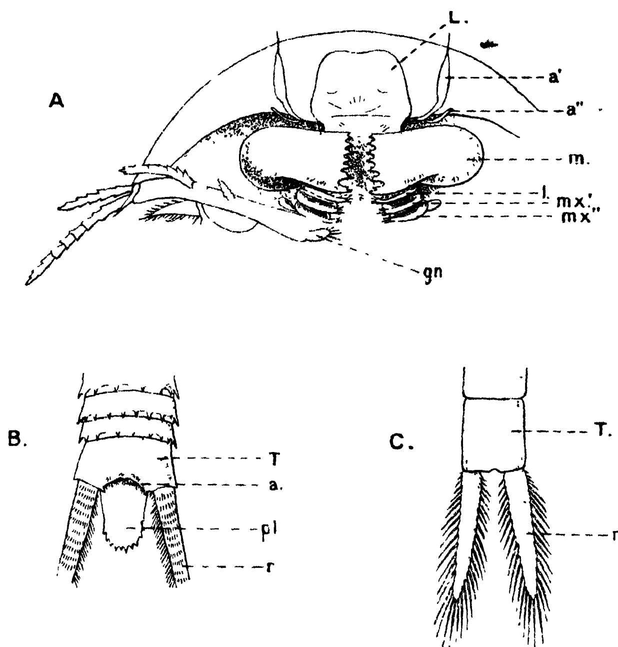


Fig. 20.

A, head-region of *Lepidurus glacialis* from below; *a'*, antennule; *a''*, antenna: *gn*, gnathobase of first trunk-limb; *L*, labrum or upper lip turned forwards (in the natural position it covers the opposed edges of the mandibles); *l*, lower lip (according to Claus, the inner lobes of the maxillulae); *m*, mandible; *mx'*, maxillula; *mx''*, maxilla. B. posterior end of body of *Lepidurus glacialis*; *a*, position of anal opening; *pl*, supra-anal plate; *r*, rami of caudal furca; *T*, terminal segment or telson. C, posterior end of body of *Branchinecta paludosa*; letters as above. (After Sars.)

between the furcal rami or, in many Cladocera, some distance in front on the dorsal surface. In the genera *Lepidurus* (Notostraca) and *Thamnocephalus* (Anostraca) the telson is produced as a thin plate above the anal opening (Fig. 20, B).

Appendages.—The *antennules* are, for the most part, purely sensory in function, not segmented or obscurely so, and carrying tufts of sensory filaments. In many Cladocera they are very small and attached to the posterior surface of the deflexed beak-like

process forming the front of the head (Fig. 18, *a'*). In the males of some Cladocera they form clasping organs for holding the female.

The *antennae* differ very much in the various orders. In the Notostraca they are vestigial (Fig. 20, A, *a''*) and may even be absent in certain species of *Apus*. In the males of the Anostraca they are converted into powerful claspers for seizing the female, and may assume extraordinary and complex forms. A pair of filaments, known as frontal appendages (Figs. 21 and 32, *f.a*), arise, in many Anostraca, from the base of the antennae, though sometimes they are inserted on the front of the head and seem quite unconnected with the antennae. They may coalesce at the base, and may be more or less ramified, adding to the complexity of the apparatus carried by the male. In the females the antennae are much simpler in form, and are probably purely sensory in function. It would seem from Claus's observations on the development of *Branchipus* that the endopodite of the antenna atrophies, and that the whole apparatus of the adult develops from the protopodite and exopodite of the larval antenna.

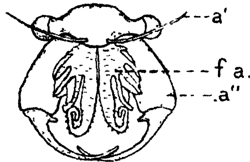


FIG. 21.

Head of *Chirocephalus diaphanus* (Anostraca) viewed from in front. (After Simon.) *a'*, antennule; *a''*, antenna; *f.a*, frontal appendages, which in this species are large and branched.

In the Conchostraca and Cladocera the antennae are large biramous swimming-organs. In the former group they have multiarticulate rami, and they are protruded ventrally between the valves of the shell (Fig. 17). In the latter order the rami have few segments, and, since the head is not enclosed between the valves of the shell, the antennae project freely (Fig. 18). In the genus *Latona* (Cladocera) a large process from the proximal segment of the exopodite causes the antenna to appear as if three-branched.

The *mandibles* (Fig. 8, C, p. 12) are devoid of palps in all existing Branchiopoda with the exception of *Polyartemia*, in which a vestigial palp has recently been found by Ekman. As a rule, they have broad toothed triturating surfaces, but in some predatory Cladocera (*Leptodora*) they become long sickle-shaped blades.

The *maxillulae* (Fig. 22, A) are of small size and simple form. As a rule, each consists of a single lobe armed with spines on the inner edge. In the Notostraca they seem to consist of two lobes, but it is possible, as Claus suggested, that the inner and anterior lobes represent the lower lip, or *paragnatha*, otherwise wanting in the group.

The *maxillae* (Fig. 22, B) are also greatly reduced and consist of a simple lobe. In the Cladocera they are entirely wanting in the adult, but a distinct rudiment is present in the embryo. In the Notostraca

an external membranous lobe is present and was formerly regarded as corresponding to the gill or *bract* of the succeeding appendages. For this reason the appendage was regarded as belonging to the series of the trunk-limbs, and was called a "foot-jaw" or "maxilliped." It has been shown, however, by Claus that the so-called "bract" is really a tubular process bearing the external opening of the maxillary gland, and is in no way related to the "bract" of the following limbs. There is therefore no reason to doubt that the appendage is homologous with the maxilla of other Branchiopoda. It is of interest to notice, in connection with the great reduction of this appendage, that there is, in *Apus*, no separate ganglion in the ventral nerve-chain corresponding to it, but that the nerves supplying it take their origin from the longitudinal connectives between the ganglia corresponding to the maxillula and the first thoracic appendage respectively.

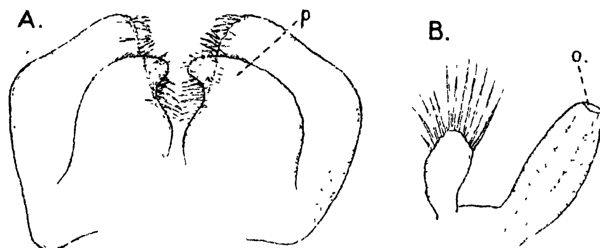
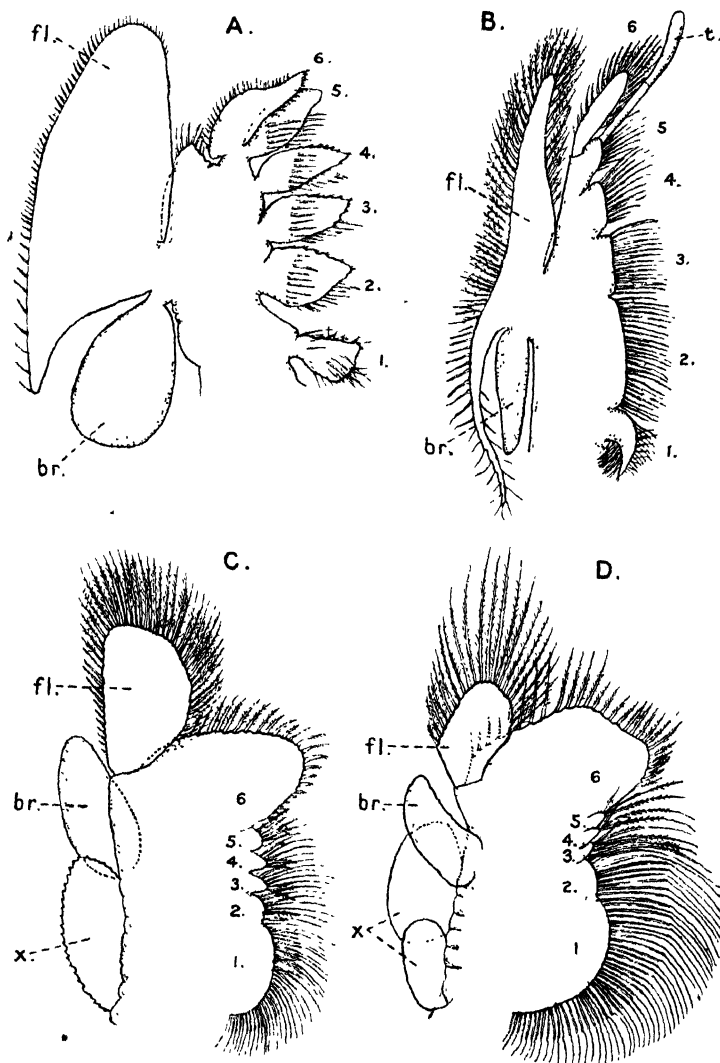


Fig. 22.

A, maxillulae, B, maxilla, of *Apus cancriformis*. (After Claus.) *p*, the so-called inner lobes of the maxillulae, representing, according to Claus, the paragnatha; *o*, opening of maxillary gland on a tubular process connected with the maxilla.

The trunk-limbs of the Branchiopoda are generally of very uniform structure, and are not grouped into definite "tagmata." On the other hand, these appendages present very great differences in the different groups composing the sub-class, and it is not easy in some cases to determine the exact homologies of the various parts.

The most primitive form is probably that found in the Notostraca (*Apus*, Fig. 23, A). Each appendage consists of a flattened corm or axis to which are attached eight lateral processes or lobes. Six of these processes spring from the inner margin of the corm and are termed *endites*, while two on the outer margin are termed *exites*. The proximal endite (1), placed near the attachment of the limb to the body, is armed with strong spines and, like some or all of the other endites, is provided with special muscles which permit of a limited amount of movement on the corm. These basal endites working against those of the opposite side function as jaws, seizing and passing forward towards the mouth particles of food which are



Trunk-limbs of various Branchiopoda. A, seventh trunk-limb of *Apus cancriformis* (Notostraca). B, third trunk-limb of *Estheria obliqua* (Conchostraca). C, fifth trunk-limb of *Branchinecta paludosa* (Anostraca). D, eleventh trunk-limb of *Polyartemia forcipata* (Anostraca). (A after Lankester; B, C, and D after Sars.) *br*, branchia or bract; *fl*, flabellum; *t*, tactile process of the fifth endite in *Estheria*; *x*, proximal exites of the Anostraca; 1-6, the six endites, of which the first is the gnathobase. Between the flabellum and the sixth endite in A is seen the "sub-apical lobe." Regarding the homology of the plate lettered *fl* in C and D, see the discussion in the text.

drawn in between them by the rhythmical movements of the appendages in swimming. They are therefore distinguished as *gnathobases*. The Branchiopoda are the only Crustacea in which gnathobases are found on limbs far removed from the mouth. Of the two exites, the distal, known as the *flabellum* (*fl*), is a thin plate with setose margins. It is moved by special muscles and probably serves chiefly as a swimming-plate. The proximal exite, known as the *bract* (*br*), is branchial in function, having a very thin cuticle, without setae, and is not provided with muscles. The end of the corm, external to the sixth endite, is produced into a rounded process, the "sub-apical lobe."

While most of the postmaxillary appendages of the Notostraca have the general structure of that just described, differing only in details of shape and proportion of the various parts, certain of them are specially modified. In the first and second pairs, the corm is divided, in the former into four, and in the latter into two segments. The endites, with the exception of the gnathobase, become more elongated in passing forwards along the series of limbs, and in the first pair the second, third, fourth, and fifth endites, counting from the base, are produced into filiform multiarticulate rami (Fig. 20, A). The fifth, in some species, is nearly as long as the body of the animal. The sixth endite, however, is much reduced and of peculiar form in the limbs of the first pair.

The trunk-limbs of the Conchostraca (Fig. 23, B) can without difficulty be compared with those of *Apus*. The six endites are distinct though reduced in size and less sharply marked off from the unsegmented corm. The gnathobase is unprovided with masticatory spines, but, like the following endites, is fringed with setae. The fifth endite is produced in some cases into a long tactile process (*t*). Only the sixth endite is marked off by a distinct articulation. The flabellum is very large and the branchia is reduced in size.

In the Anostraca (Fig. 23, C, D) the structure of the parts is rather different and their exact homologies are not quite clear. The flattened unsegmented corm has its inner edge more or less distinctly divided into six lobes. At the distal end, towards the outer side, is a broad oval plate (*fl*) defined by a well-marked articulation and fringed with setae. On the proximal side of this, on the outer edge, is the branchia, characterised as such by its thin cuticle and by the lack of setae. Still nearer the base the outer margin of the corm is produced into a rounded plate (*x*), very thin and not defined by an articulation. In *Polyartemia* and in some species, at least, of *Chirocephalus* there are two such plates (Fig. 23, D). It appears most probable that the six lobes of the inner edge correspond to the six endites of the Notostracan limb, in which case the distal setose plate (*fl*) will represent

the flabellum. This view, however, is not accepted by Sars, who regards the distal setose plate as the sixth endite and supposes that the flabellum is wanting in the Anostraca. Sars's interpretation gains some support from a comparison with the Conchostracan type of limb, where the sixth endite has much the same position as the setose plate of the Anostraca. It is further supported by the fact that, in the development of the limbs of *Apus*, the flabellum only appears after some of the endites have become marked off, while in *Branchipus* the first differentiation to take place in the limb-buds is a bifurcation defining the distal setose plate from the terminal lobe of the inner edge. In any case it seems certain that the external basal plate or plates of the Anostraca are new formations unrepresented in the Notostraca and Conchostraca, and not, as Lankester supposed, homologous with the branchia (or bract) of these groups.

In the Cladocera the structure of the limbs is still more difficult to interpret. In the Ctenopoda (Fig. 24, A), where the six pairs of "thoracic" appendages are comparatively uniform, the inner margin forms a small gnathobasic lobe followed by a broad lobe carrying a comb-like series of long setae. A distal lobe may correspond to the flabellum of *Apus* and *Estheria*, or perhaps to the sixth endite. The branchia is present and has the usual characters. In the Anomopoda there is considerable differentiation among the members of the series. In *Daphnia*, for example, the first limb (Fig. 24, B) is obscurely segmented and the five lobes on the inner edge are slightly developed. The second limb (Fig. 24, C) has the gnathobase enlarged and has an outer branch regarded as the exopodite. Both of these limbs are adapted by the possession of long curved setae to aid in the prehension of food. The third (Fig. 24, D) and fourth pairs are characterised by the great development of the proximal endite with its comb-like row of setae. They serve to keep a current of water flowing between the valves of the shell for the purposes of respiration and feeding. The last pair in *Daphnia* are greatly reduced (Fig. 24, E).

In the Gymnomera, and especially in *Leptodora* (Fig. 19), the trunk-limbs have lost the characteristic leaf-like shape and have become cylindrical, elongated, and divided into four well-marked segments, without any trace of endites or exites, serving only for seizing and holding prey.

Modifications of certain of the trunk-limbs subservient to the processes of reproduction are found in all divisions of the Branchiopoda. In the males of most of the Conchostraca the first two pairs have the terminal portion modified into a cheliform clasper (Fig. 17, B), but in *Limnetis* and in the Cladocera only the first pair is so modified. Sexual modifications of trunk-limbs in the female are found only in the Notostraca and in some Conchostraca.

In the former the appendages of the genital somite (the eleventh trunk-somite) are modified to form brood-pouches, and are known as "oostegopods" (Fig. 25). The sixth endite is coalesced with

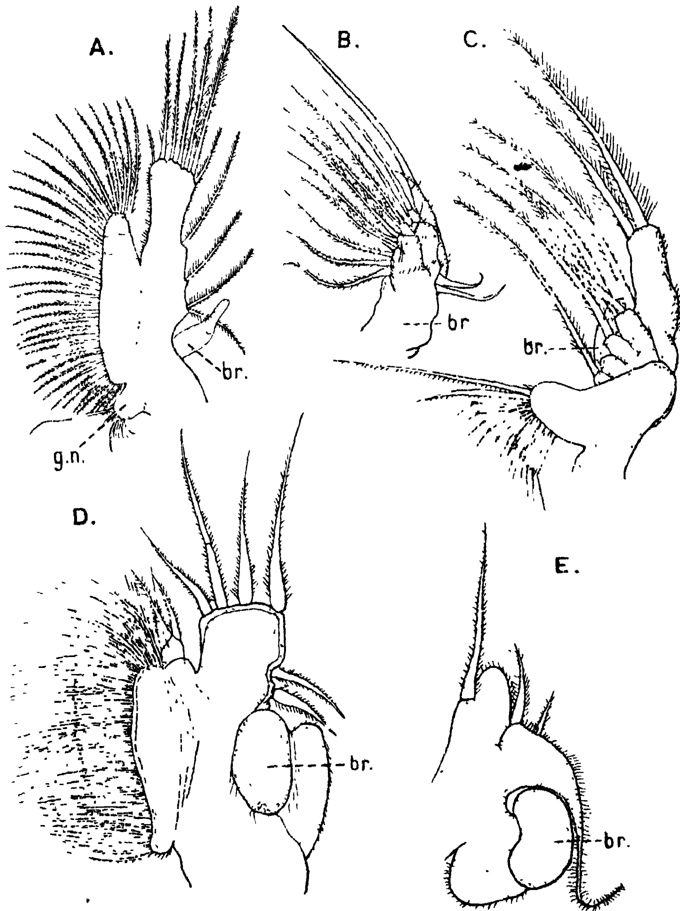


Fig. 24.

Trunk-limbs of Cladocera. A, first trunk-limb of *Sida crystallina* (Ctenopoda). B, first, C, second, D, third, E, fifth trunk-limbs of *Daphnia pulex* (Anomopoda). *br*, branchia; *gn*, gnathobase. (After Lilljeborg.)

the sub-apical lobe, and together with it forms a hemispherical cup, closed by a movable lid formed by the flabellum. In some species of Conchostraca two or three pairs of limbs near the genital apertures have the proximal division of the flabellum produced

and thickened, and to this the egg-masses are attached between the valves of the shell.

As regards the homologies of the parts of the Branchiopod-limb with those of the biramous type found in other Crustacea, two views have been suggested. According to the interpretation adopted by Huxley, among others, the "flabellum" or distal exite of the *Apus*-limb corresponds to the exopodite, while the distal part of the corm represents the endopodite. Lankester, on the other hand, considers the endopodite and the exopodite to be represented by the fifth and sixth endites respectively, the corm being the protopodite and the flabellum the epipodite. The former view is supported by a comparison with the leaf-like thoracic limbs of the Leptostraca, while Lankester's interpretation is based chiefly on a comparison of the pre-oral with the post-oral appendages in the larval *Apus*, and of the trunk-limbs of *Apus* with the maxilla and maxillipeds of various Decapods. Neither view is quite free from difficulties, and the divergences in structure mentioned above as occurring in the Anostraca still further complicate the matter, which requires further investigation.

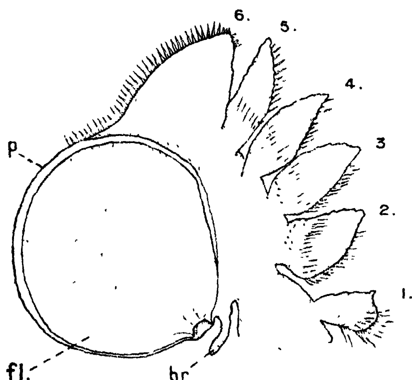


FIG. 25.

Eleventh trunk-limb or oostegopod of *Apus cancriformis*, female. (After Lankester.) 1-6, the six endites, of which the sixth is fused with the "sub-apical lobe" which forms the pouch, *p*, containing the eggs; *fl*, flabellum forming the cover of the pouch; *br*, the vestigial bract.

Alimentary System.—The oesophagus is narrow and is provided with constrictor and dilator as well as longitudinal muscles. It usually projects a little way into the more capacious mid-gut, and in *Polyartemia* the terminal part is armed with setae. The hind-gut is short and muscular. In the aberrant Cladoceran *Leptodora* the oesophagus is of great length and the mid-gut hardly extends in front of the terminal segment of the body. In many Cladocera belonging to the families Lyncodaphnidae and Lynceidae the mid-gut is more or less coiled, forming a simple loop or a spiral

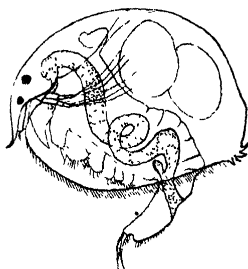


FIG. 26.

Pleuroxus uncinatus (Cladocera) (after Lilljeborg), showing the coiled intestine and its ventral diverticulum.

of one and a half turns (Fig. 26). As a rule, the anterior part of the mid-gut gives off a pair of diverticula. In the Notostraca and Conchostraca these are much ramified, and in the Anostraca they are saccular and lobulated. In the Cladocera they are often absent, and when present are simple caeca. In some Cladocera of the family Lynceidae the posterior part of the alimentary canal gives off an unpaired diverticulum on the ventral side (Fig. 26). It is usually short, but sometimes it is of considerable length. It is stated to arise from the hind-gut, and its walls contain large gland-cells.

Circulatory System.—Except in the Cladocera, the heart is elongated and tubular. In the Anostraca it traverses almost the whole length of the trunk, and has paired ostia in each somite except the first and last. In the Notostraca the heart extends through the first eleven trunk-somites and has eleven pairs of ostia. In the Conchostraca it is restricted to three or four somites, with a corresponding number of ostia. In the Cladocera the heart is greatly abbreviated, forming a sub-globular sac with a single pair of ostia, lying in the region of the first trunk-somite (Fig. 18, *h*). There are no distinct vessels and the blood is discharged directly from the anterior end of the heart (through three openings in the Notostraca) into the sinuses of the head-region.

In some genera (*Apus*, *Branchipus*, *Artemia*, and some Cladocera) the fluid of the blood is coloured red, owing, as Lankester has shown, to the presence of haemoglobin.

Excretory System.—The maxillary gland (Fig. 18, *gl*) is well developed in all Branchiopoda. Except in the Anostraca and some aberrant Cladocera (*Leptodora*), it lies within the thickness of the shell-fold. It shows the typical structure, consisting of end-sac, glandular coiled tube, and short terminal duct. In the Notostraca, as already mentioned, the external opening is at the end of a tubular process arising from the under side of the head, close to the maxilla.

The antennal gland is well developed in the larval stages of Anostraca, Notostraca, and Conchostraca (Fig. 10). A vestige of it persists in the adult *Artemia*.

Glands.—Belonging to the dermal series of glands are the segmentally arranged ventral and leg glands of some Anostraca, and the groups of unicellular glands in the labrum which are probably always present.

Special interest attaches to the structure variously referred to as "neck gland," "dorsal organ," or "adhesive organ," found in many Branchiopoda. In its simplest form this consists of a thickened and glandular area of the ectoderm, on the dorsal surface near the posterior limit of the head-region. The adhesive secretion reaches the exterior through pores or slits in the cuticle, and is used

for the purpose of attaching the animal temporarily to plants or other objects. In the Notostraca, however, where the organ is apparently well developed, it is not used for this purpose. In the Anostraca it is absent in the adult, though very large in the larva. In some of the Conchostraca (*Limnadia*) it is prominent and pedunculated. In many Cladocera it is greatly reduced or absent, but in some it is large and functional. In the Sididae the organ is divided into three parts, a large median anterior and a pair of smaller ones posterior to it. In this case certain muscles attached to the integument in the neighbourhood of the organ are believed to produce a sucker-like action, thus aiding adhesion. In some Lynceidae two organs are found, one behind the other.

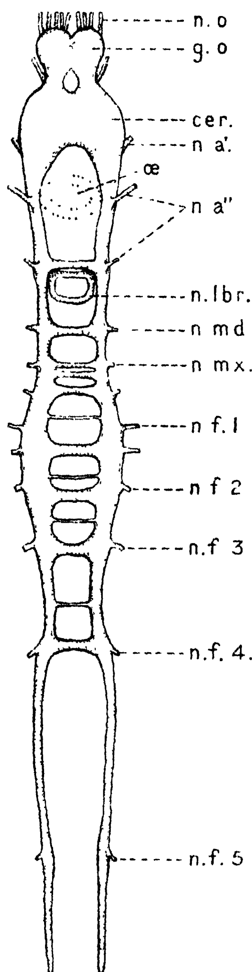


FIG. 27

Nervous system of *Simocephalus* (Cladocera) from the dorsal side. (After Cunnington.) *cer*, brain; *g.o*, optic ganglia, here partly fused in correlation with the fusion of the paired eyes; *n a'*, nerve to antennule; *n.a''*, nerves to antennae, arising from the oesophageal connectives; *n.f.*1–*n.f.*5, nerves to the five trunk-limbs; *n.lbr*, nerve ring encircling oesophagus in region of the labrum; *n.md*, nerve to mandibles; *n.mx*, nerve to maxillulae; *n.o*, optic nerves; *oe*, position where oesophagus passes between the nerve-cords; ventrally the oesophagus curves backwards so as to pass through the ring *n.lbr* before reaching the mouth. The transverse commissure corresponding to the antennal ganglia is on a level with the roots of the posterior antennal nerves.

Endoskeletal Structures.—In many Branchiopoda there is a considerable development of trabeculae and plates of tendinous connective tissue giving attachment to muscles. This system, which almost merits the name of endoskeleton, is most fully developed in the Anostraca, where the external cuticle remains almost membranous, but it is also found in the Cladocera. In the Notostraca the chief part of this endoskeletal system is a tendinous plate, known as the *entosternite*, lying under the anterior part of the alimentary canal and giving attachment to the adductors of the mandibles and to other muscles.

Muscular System.—In the Conchostraca and Cladocera the valves of the shell are drawn together by a transverse adductor muscle. In some, at least, of the Cladocera this muscle is double.

Nervous System.—As has been mentioned above, the nervous system of most Branchiopoda shows very primitive characters in the ladder-like form of the ventral nerve-chain (Fig. 11, p. 17, and Fig 27). In some Cladocera, however (Polyphemidae and *Leptodora*), the ventral ganglia are more or less coalesced into a single mass. In all cases, the nerves to the antennae arise not from the supra-oesophageal ganglia, but from the first post-oesophageal pair of ganglia. This pair of ganglia is quite distinct from the next succeeding pair, which innervate the muscles of the mandibles, and, like all the ventral pairs of ganglia (with the occasional exception of the mandibular), it has a double transverse commissure. It is closely connected with the origin of a "visceral" nerve-ring which encircles the oesophagus and bears an unpaired ganglion in the region of the labrum (Figs. 27 and 28, *n.lbr*). So far as their nerve-supply is concerned the antennae are, in the Branchiopoda, unmistakably post-oral. In the Notostraca the nerves of the antennules (Fig. 28, *n.a'*) arise from the oesophageal connectives just in front of those of the antennae. This was supposed by Lankester to be a primitive condition indicating the post-oral origin of these appendages. Pelseneer showed, however, that the fibres of these nerves pass forward to a pair of nerve-centres in the supra-oesophageal ganglion. In the other Branchiopoda the corresponding nerves arise from the posterior part of the brain, and there can be little doubt that the condition in *Apus* is a secondary one due to the brain having been shifted forwards and upwards in company with the paired eyes which lie on the dorsal surface of the head, while the antennules are inserted on its lower surface. In *Apus* there is no ganglion corresponding to the reduced maxillae, and these limbs receive a pair of nerves arising from the longitudinal connective between the maxillular and first thoracic ganglia (Fig. 28, *n.mx''*). In the Cladocera, also, where the maxillae are quite rudimentary or absent, there is no ganglion corresponding to this somite. In *Branchipus*, however, there is a distinct pair of ganglia with double transverse commissures.

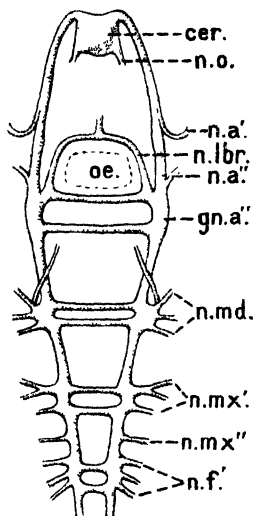


FIG. 28.

Anterior part of the central nervous system of *Apus*, from below, semi-diagrammatic. *cer*, brain; *gn.a''*, antennal ganglion; *n.a'*, nerve to antennule; *n.a''*, nerve to antenna; *n.f'*, nerves to first trunk-limb; *n.lbr*, nerve-ring encircling oesophagus; *n.md*, nerves to mandible; *n.mx'*, nerves to maxillula; *n.mx''*, nerve to maxilla; *oe*, position of oesophagus. (After Lankester and Pelseneer.)

Sense-Organs.—The compound eyes are present in all Branchiopoda. In the Anostraca they are elevated on movable peduncles, but in all other Branchiopoda they are sessile, preserving, however, a certain degree of mobility owing to the fact that they are sunk below the surface and covered by an invagination of the outer cuticle, the cavity of the invagination generally remaining in communication with the exterior by a pore (Fig. 29). Except in the Anostraca, the two eyes are closely approximated; and in some Conchostraca, and more completely in the Cladocera, they fuse together into a single eye. The cornea is not distinctly faceted. The crystalline cone is divided into four parts. The rhabdom is surrounded by five rhabdom-cells, but (in *Branchipus*) is not distinctly divided into rhabdomeres.

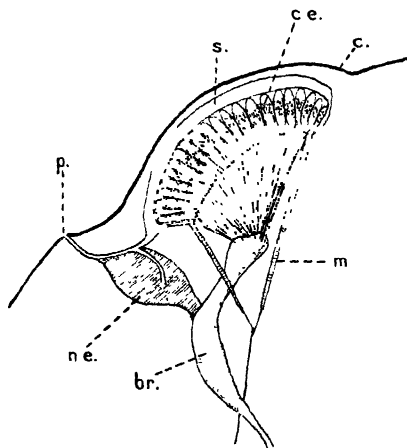


Fig. 29.

Diagrammatic longitudinal section through the compound eye and associated structures of *Apus*. (After Bernard.) *br*, brain; *c*, external cuticle of head; *c.e*, compound eye; *m*, muscle for moving compound eye; *n.e*, nauplius eye; *p*, pore leading into the water-sac covering the compound eye and sending a blind diverticulum into the nauplius eye; *s*, the water-sac, formed by an invagination of the integument. The pore, *p*, is in the median line, so that, as a matter of fact, a strictly longitudinal section passing through it would pass *between* the compound eyes.

Except in some of the Cladocera, the nauplius eye persists in the adult of all Branchiopoda (Figs. 18 and 29, *n.e*). It is of the usual tripartite structure, and may be connected with the brain by three separate nerves or by a single one. In the Cladocera it is reduced in size and simplified in structure, and may be entirely absent.

Frontal Organs.—In *Branchipus* a pair of organs, presumably sensory, lie on the front surface of the head (Fig. 5, *f*). Each consists of a large hypodermis cell surrounded by a group of ganglion cells and connected with the brain. Below this, in *Branchipus*, is a group of club-shaped cells containing peculiarly shaped rod-like bodies and connected with nerves. In the Cladocera the first-mentioned frontal organs are vestigial, and appear to be represented by a group of cells supplied by a continuation of the nerve of the median eye. The club-shaped cells, however (the "*Nackenorgan*" of Leydig), are well developed, but are situated high up on the sides or on the dorsal surface of the head. The pair of nerves supplying them originate from the ventral surface of the brain.

Reproductive System.—The gonads are generally paired, but in some Cladocera they may be united in the middle line. In the Notostraca they are much ramified, but in the other Branchiopoda they are of simple tubular form. Probably all Branchiopoda are of separate sexes. In the Notostraca Bernard has described testicular tissue in the ovary, but the occurrence of normal functional hermaphroditism is still unproved.

In the Notostraca the genital ducts open on the 11th trunk-somite, and this is probably also the case in all the Conchostraca. In the majority of the Anostraca the first two apodous somites, namely, the 12th and 13th of the trunk, are more or less completely fused, forming a "genital segment" on which the genital ducts open. The development indicates that the openings probably belong to the 12th somite. In *Polyartemia*, however, the leg-bearing somites are 19 in number, and the 20th and 21st somites form the genital segment in the male sex. In the female all the apodous segments are coalesced. In the Cladocera the female genital apertures are lateral or dorsal in position on the posterior apodous division of the body. The male apertures are lateral or ventral and often placed farther back, sometimes quite at the end of the body.

The genital openings are generally paired, but the female opening is unpaired in the Anostraca, where the oviducts unite to form a uterine chamber (Fig. 15, A, *ut*) with groups of gland-cells on its walls. In some Cladocera the male opening is unpaired. The terminal part of the vasa deferentia forms a paired eversible intromittent organ in the Anostraca (Fig. 15, B, *p*) and in some Cladocera (Sididae).

The spermatozoa are immobile and usually spherical. In the Cladocera, however, they present a remarkable variety of form, differing greatly sometimes even in the species of one genus.

In the Anostraca the eggs are retained, sometimes till they hatch, in the uterine portion of the oviduct. In the other Branchiopoda they are carried after extrusion either in special receptacles formed by the 11th pair of trunk-limbs (Notostraca) or enclosed within the valves of the shell (Conchostraca and Cladocera). In the Conchostraca the egg-masses are attached to certain pairs of specially modified trunk-limbs. In the Cladocera a special brood-chamber is formed between the dorsal surface of the body and the shell, and is closed behind by fleshy folds or prominences. Further, in some Cladocera, if not all, a modification of the hypodermis of the dorsal surface takes place for the secretion of a nutritive fluid by which the embryos are nourished within the brood-chamber. In the Cladocera the sexually produced "resting"- or "winter"-eggs are deposited within the cast-off shell, and in many a part of the shell becomes thickened and indurated, and

separates from the rest at ecdysis to form a protective case known as the *ephippium*, containing the resting-eggs.

DEVELOPMENT.

Excepting the great majority of the Cladocera and a few Conchostraca (*Cyclestheria*) in which the development is embryonic,

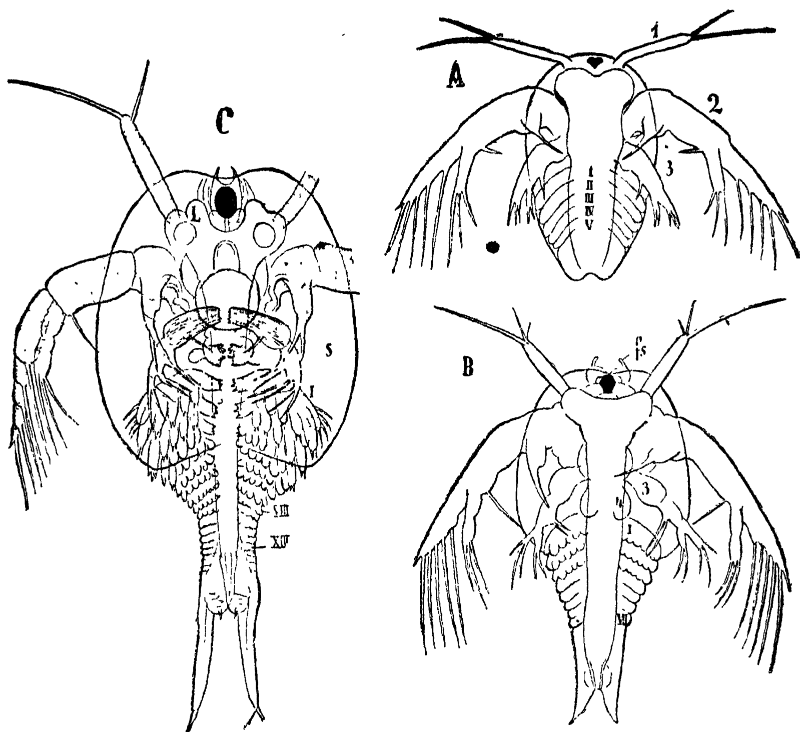


FIG. 30.

Larval stages of *Apus cancriformis*. A, metanauplius, just hatched; B, "second" larval stage; C, "fourth" larval stage. 1, antennule; 2, antenna; 3, mandible; 4, maxillula; I-XIII, first thirteen trunk-somites; *f.s*, frontal sense-organ; *L*, hepatic diverticula; *s*, carapace. (After Claus, from Korschelt and Heider's *Embryology*.)

the Branchiopoda have a free-swimming nauplius or metanauplius stage. Some differences exist even in closely allied forms in the stage of development reached at hatching. In the Notostraca (Fig. 30) and Anostraca the larva is a typical metanauplius with an oval body, showing posteriorly the commencing division of several trunk-somites and sometimes rudiments of their appendages. The antennules are well developed, but simple. The antennae have a movable masticatory process. The corresponding

process of the mandible is feebly developed. The paired frontal sense-organs in the form of papillae develop at an early stage, though not present on hatching. The maxillulae and maxillae are generally not marked off till after the succeeding limbs have been differentiated. The "dorsal organ" or nuchal gland is very large in the early stages even in those forms in which it is greatly reduced or absent in the adult. The trunk-somites and their appendages become differentiated in regular order from before backwards.

In the Conchostraca the earliest larva has no trace of the trunk-somites. The antennules are greatly reduced and the labrum is very large. The nauplius of *Limnetis* is remarkable for the broad dorsal shield and for the peculiar cruciform shape of the front of the head. In the Conchostraca and in the Cladocera the shell develops from paired rudiments. The later larval stages of

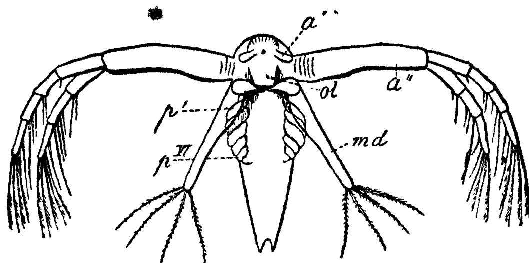


Fig. 31.

Metanauplius of *Leptodora*, hatched from a "winter"-egg. *a'*, antennule; *a''*, antenna; *md*, mandibular palp; *ol*, labrum; *pi-pvi*, rudiments of the six pairs of trunk-limbs. (After Sars, from Korschelt and Heider's *Embryology*.)

the Conchostraca, as, for instance, *Estheria*, correspond very closely with the adult structure of the Cladocera.

In the Cladocera the eggs are usually large and rich in yolk, or, when the reverse is the case, a special provision is made for the nourishment of the developing embryos within the brood-chamber. The egg-membrane, which in the parthenogenetic ("summer") eggs is very thin, is early cast off, and the developing embryos lie free within the brood-chamber. In the sexually produced ("winter" or "resting") eggs the whole development is gone through within the egg-membrane. A distinct *nauplius* stage is passed through, and, at least in some cases, is marked by the formation of a cuticle which is cast off later. The rudiments of the maxillulae and maxillae do not appear until after some of the trunk-limbs have already appeared, and the maxillae afterwards become reduced and disappear in the adult. In the embryos of some Cladocera in which only five pairs of trunk-limbs are present in the adult, six pairs of rudiments are formed, but the last pair disappears later.

The young of the Conchostracan *Cyclestheria* have an embryonic development very similar to that of Cladocera within the shell of the parent.

A remarkable exception to the rule of embryonic development among Cladocera is afforded by the aberrant genus *Leptodora*. The parthenogenetic "summer"-eggs develop in the usual way within the brood-pouch of the parent. The "winter"-eggs, however, hatch out as *metanauplii* (Fig. 31). The body is unsegmented, but the six pairs of thoracic limbs are already visible as rudiments. The antennules are very short. The antennae, on the other hand, are unusually large, as they are also in the adult. They are without any masticatory process. The mandibles have long unsegmented palps. The compound eyes are not yet developed, but the nauplius eye is present, and persists throughout life in the individuals hatched from "winter"-eggs, while it is absent in those hatched from the "summer"-eggs. In the reduction of the antennules this larva shows some resemblance to that of *Estheria*.

Remarks on Habits, etc.

The great majority of the Branchiopoda inhabit fresh water. A few species of Cladocera, belonging to three genera, occur in the sea, and the Anostracan *Artemia* is found in salt lakes and brine-pools. The Cladocera form an important part of the plankton of lakes and ponds, and the larger Anostraca, Notostraca, and Conchostraca occur chiefly in small ponds and rain-water pools. The occurrence, throughout the group, of sexually produced, thick-shelled "resting"-eggs, which can survive desiccation, in addition to the thin-shelled eggs produced by parthenogenesis, probably indicates the very ancient adaptation of the Branchiopoda to a freshwater habitat.

No parasitic Branchiopoda are known.

The Cladocera are nearly all of microscopic size, and some species which do not exceed 0·25 mm. in length are among the smallest known Arthropoda. Of the other orders, the Notostraca comprise the largest forms, some species of *Apus* reaching 70 mm. in length.

Palaeontology.

The Conchostraca are well known as fossils, and forms referred to the existing genus *Estheria* occur as early as the Devonian. The Notostraca are more doubtfully represented by *Protocaris* from the Lower Cambrian. From the delicacy of their structure, the Anostraca are less likely to be preserved, and almost the only undoubted example is *Branchipodites* of the Oligocene. The Cladocera are not certainly known earlier than Post-tertiary deposits.

Many palaeozoic fossils formerly classed with the "Phyllopoda" are now referred to the Phyllocarida.

Affinities and Classification.

The alliance of the groups included in the Branchiopoda is justified especially by the lobed foliaceous form of the trunk-limbs which they have in common, but the divergences of structure in other respects are greater than is the case in other sub-classes of Crustacea. Thus, while the other sub-classes are more or less strictly nomomeristic, each of the orders of Branchiopoda, and even some of the families and genera, are markedly anomomeristic. This is in agreement with the view that the Branchiopoda are a primitive group which has not attained to the fixity of general structure found in the other sub-classes.

Their primitive character is further shown, as has been pointed out, by the general uniformity of the trunk-somites and their appendages, by the presence of gnathobases on all the trunk-limbs, by the "ladder-like" form of the ventral nerve-chain and the post-oral position of the antennal ganglia, and by the tubular heart and its segmentally arranged ostia. The primitive character of the larval development has also been alluded to.

It may be mentioned here that, as in other groups of Arthropoda, the possession by many Branchiopoda of a large number of somites can hardly be regarded as proof of their primitive position. In the Notostraca, the fact that the posterior pairs of appendages exceed in number the somites which carry them, shows that secondary changes, whether by coalescence of somites or, more probably, by multiplication of appendages, have taken place. A further argument in favour of a possible increase in number of somites is afforded by a consideration of the aberrant Notostracan genus *Polyartemia* (Fig. 32). Apart from the Cladocera, which the abbreviation of the trunk excludes from the comparison, *Polyartemia* forms the only exception to the rule that the genital apertures of the Branchiopoda are situated, approximately, in the region of the twelfth trunk-somite. Now, the close resemblance in all other respects between *Polyartemia* and the other Anostraca strongly suggests that the nineteen somites interposed between the head and the genital somite in that genus correspond, as a whole, to the eleven somites which occupy the same position in the other Anostraca; and the agreement of the latter in this respect with most of the other Branchiopoda seems to indicate that the smaller number of somites is here the more primitive, the larger the more specialised condition. If this be so, a similar multiplication of somites in the post-genital region of Notostraca may well account for the exceptionally large number found in that order.

The classification of the Branchiopoda commonly adopted differs from that given below in grouping together the Anostraca, Notostraca, and Conchostraca as a single order, Phyllopoda (Latreille, 1802),[1] distinguished from the Cladocera chiefly by the greater number of somites and appendages and by the prevalence of metamorphosis in development. The groups of the Phyllopoda,

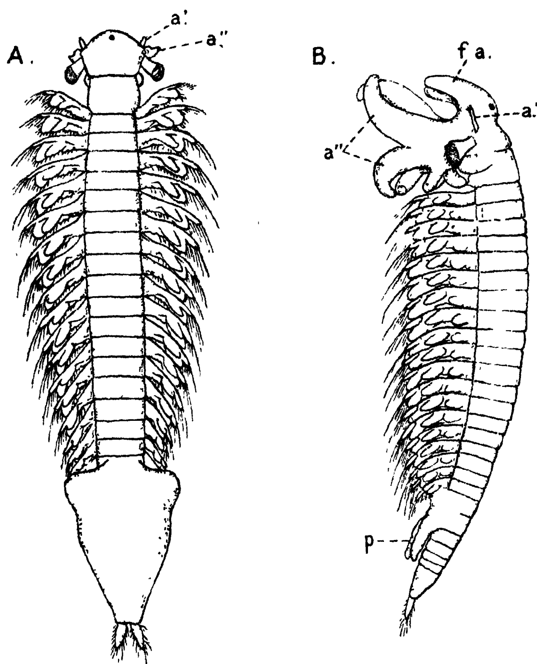


FIG. 32.

Polyartemia forcipata, one of the Anostraca. × 5. (After Sars.) A, female, dorsal view; B, male, lateral view. *a'*, antennules; *a''*, antennae, very small in the female but greatly enlarged and three-branched in the male; *f.a*, "frontal appendage"; *p*, paired penes of the male. There are nineteen limb-bearing trunk-somites, followed, in the male, by six limbless somites (besides the telson), of which the first and second are partly coalesced to form the genital segment. In the female the limbless region of the trunk is unsegmented.

however, differ among themselves in characters which are at least as important as those separating the Cladocera from the Conchostraca, and it seems desirable to recognise this by giving them the rank of orders.

[1] Unfortunately some writers, following Claus, have transposed the names Branchiopoda and Phyllopoda, applying the latter to the sub-class and the former to one of its divisions, but this use is not sanctioned either by priority or by universal custom.

SUB-CLASS BRANCHIOPODA.

ORDER 1. **Anostraca.**

Carapace absent; paired eyes pedunculate; antennae prehensile in male, reduced in female; trunk-limbs, 11 or 19 pairs, none post-genital; furcal rami unsegmented; development with metamorphosis.

Family POLYARTEMIIDAE. *Polyartemia*, Fischer (Fig. 32). Family BRANCHIPODIDAE. *Branchipus*, Schäffer; *Chirocephalus*, Prévost (Fig. 21); *Artemia*, Leach; *Branchinecta*, Verrill (Fig. 15). Family THAMNOCEPHALIDAE. *Thamnocephalus*, Packard.

ORDER 2. **Notostraca.**

Carapace forming a dorsal shield; paired eyes sessile; antennae vestigial; trunk-limbs, 40 to 63 pairs, of which 29 to 52 are post-genital; furcal rami multiarticulate; development with metamorphosis.

Family APODIDAE. *Apus*, Latreille; *Lepidurus*, Leach (Fig. 16).

ORDER 3. **Conchostraca.**

Carapace bivalved, enclosing head and body; paired eyes sessile, coalescent; antennae biramous, natatory; trunk limbs, 10 to 27 pairs, of which 0 to 16 are post-genital; furcal rami claw-like; development usually with metamorphosis.

Family LIMNADIIDAE. *Limnadia*, Brongniart; *Estheria*, Ruppel (Fig. 17); *Cyclestheria*, G. O. Sars. Family LIMNETIDAE. *Limnetis*, Lovén.

ORDER 4. **Cladocera.**

Carapace bivalved, generally enclosing body but leaving head free, sometimes reduced and serving only as a brood-sac; paired eyes sessile, coalesced; antennae biramous (except in the female *Holopedium*), natatory; trunk-limbs, 4 to 6 pairs, none of which are post-genital; furcal rami claw-like; development embryonic, rarely with metamorphosis.

SUB-ORDER 1. CALYPTOMERA.

Carapace completely enclosing body and limbs.

Tribe 1. CTENOPODA. Six pairs of trunk-limbs all similar and foliaceous.

Family SIDIDAE. *Sida*, Straus; *Latona*, Straus; *Penilia*, Dana. Family HOLOPEDIIDAE. *Holopedium*, Zaddach.

Tribe 2. ANOMOPODA. Five or six pairs of trunk-limbs, first two pairs more or less prehensile.

Family DAPHNIIDAE. *Daphnia*, O. F. Muller (Fig. 18); *Moina*, Baird; *Simocephalus*, Schodler (*Simosa*, Norman). Family BOSMINIDAE. *Bosmina*, Baird. Family LYNCODAPHNIIDAE. *Ilyocryptus*, G. O. Sars; *Macrothrix*, Baird. Family LYNCEIDAE. *Lynceus*, O. F. Müller; *Chydorus*, Leach; *Eurycercus*, Baird; *Pleuroxus*, Baird (Fig. 26); *Monospilus*, G. O. Sars.

SUB-ORDER 2. GYMNOMERA.

Carapace not enclosing body and limbs.

Tribe 1. ONYCHOPODA. Four pairs of trunk-limbs, more or less compressed.

Family POLYPHEMIDAE. *Polyphemus*, O. F. Muller; *Bythotrephes*, Leydig; *Evadne*, Lovén; *Podon*, Lilljeborg.

Tribe 2. HAPLOPODA. Six pairs of trunk-limbs, completely pediform.

Family LEPTODORIDAE. *Leptodora*, Lilljeborg (Fig. 19).

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CHAPTER III

THE OSTRACODA

SUB-CLASS OSTRACODA, Latreille (1802).

Order 1. **Myodocopa.**
,, 2. **Cladocopa.**
,, 3. **Podocopa.**
,, 4. **Platycopa.**

Definition.—Crustacea in which the carapace forms a bivalve shell; the trunk is indistinctly segmented, its posterior part is without limbs and ends in a caudal furca; the antennules and antennae are large and used for locomotion; the mandibles have a palp; not more than four pairs of limbs are distinctly developed behind the mandibles and they vary much in form; the genital apertures are behind the last pair of limbs; the paired eyes are sometimes present; development with metamorphosis, the young hatched in the form of a modified nauplius.

Historical.—Although various species of Ostracoda were seen and figured by the early microscopists, the scientific study of the group may be said to begin with O. F. Müller's *Entomostraca* (1785). The bivalve shell caused these animals to be associated in most of the earlier systems of classification with the Cladocera, from which they were separated by Milne-Edwards (1840). Almost the first to give an account of the internal anatomy was Zenker. The knowledge of their development is based chiefly on the works of Claus. The systematic and faunistic works of G. O. Sars, Brady, and Norman are among the most important; while in recent years G. W. Müller has made noteworthy advances towards a precise and detailed knowledge of morphology and classification.

MORPHOLOGY.

bivalved shell which completely encloses the body and limbs is usually elliptical in outline as seen from the side, often somewhat flattened ventrally, but it may be nearly

globular or, in some Halocypridae, greatly elongated. The two valves are probably always more or less unsymmetrical, especially along the ventral margin. On the dorsal side they are connected by a hinge-joint, which may be merely an uncalcified strip of the integument (Halocypridae), or may be strengthened by interlocking ridges and teeth. The most complex hinges are found among the Cytheridae. The almost globular shell of *Gigantocypris* is exceptional in that the free edges of the valves occupy only about one-third of the circumference.

The outer surface of the valves is seldom quite smooth. It may be beset with setae or pitted or sculptured (Fig. 33, C), and is sometimes produced into wing-like processes. When the shell is strongly calcified and opaque more transparent spots may mark the position of the eyes (Podocopa, Fig. 33, *e*). The attachment of the adductor muscle is usually visible externally as a group of

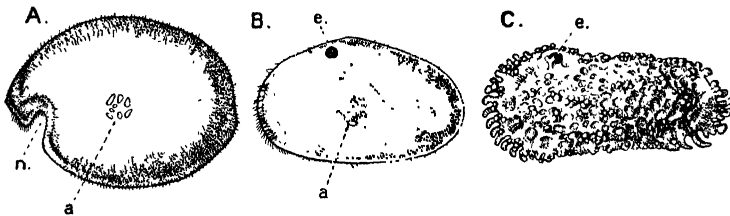


FIG. 33.

Lateral view of shell of A, *Philomedes brenda* (Myodocopa), × 8 ; B, *Cypris fuscata* (Podocopa), × 19 ; C, *Cythereis ornata* (Podocopa), × 33. *a*, attachment of adductor muscles ; *e*, median eye ; *n*, antennal notch. (A after Brady and Norman ; B and C after G. W. Muller.)

spots, the arrangement of which affords characters of systematic importance (*a*). When the edges of the valves are brought together they usually fit closely, but in some cases openings are left. The most important of these is the "antennal notch" found in most Myodocopa, and permitting the protrusion of the antennae (Fig. 33, A, *n*). Unicellular glands opening by pores on the surface of the shell are frequent in Myodocopa, less so in Podocopa.

The fold which marks off the shell from the body on each side does not extend very far towards the dorsal surface, and certain of the viscera may extend, as in some Cirripedia, into the cavity between the outer and inner integument of each valve. This is the case with the hepatic caeca in some Cyprididae (Pontocyprinae), and more commonly with the reproductive organs, especially the ovaries, which in the Cyprididae are completely and in the Cytheridae partly lodged in the cavity of the shell-fold. In the Cypridinidae a network of blood-channels traverses each valve, radiating outwards from the muscle-impression.

The posterior part of the body, which is free within the shell,

shows, at most, only indistinct traces of segmentation (*Cytherella*). The terminal part is curved ventrally, and ends in a caudal furca. In the Myodocopa the furcal rami are flattened triangular plates, with short, stout spines or teeth on the hinder margins (Fig. 37, E). In the Podocopa they are slender or styliform, bearing setae, or may be much reduced, as in the Cytheridae.

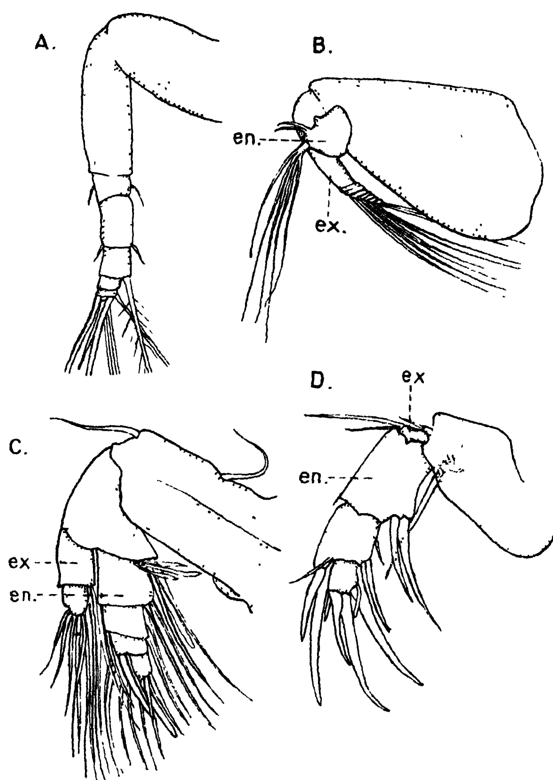


Fig. 34.

A, antennule of *Cypridina mediterranea*, ♀. B, antenna of *Conchoecia magna*, ♀. C, antenna of *Cytherella sordida*. D, antenna of *Darwinula stevensoni*. (After G. W. Muller.) *en*, endopodite, *ex*, exopodite, according to Muller's interpretation.

Appendages.—The *antennules* may function as sensory organs, or they may be used for swimming, creeping, or digging in sand, and their form and armature of setae or spines are correspondingly varied. Each is composed of eight segments in *Cypridina* (Fig. 34, A) and in *Pontocypris*, and this seems to be the typical number from which the others have been derived by reduction. In the Halocypridae the segments are reduced to two or one. Sometimes

the antennules are modified in the male sex as organs for clasping the female. This appears to be the function of certain highly peculiar setae provided with sucker-like organs found in the male of *Cypridina*.

With very few exceptions the *antenna* appears to be the chief organ of locomotion, whether swimming or creeping. In the Myodocopa it is biramous, and the outer branch is more strongly developed than the inner, with eight or nine segments carrying natatory setae. The inner branch has not more than three segments, and is often modified as a clasping organ in the male. It is characteristic of the Myodocopa that the single segment of the peduncle is greatly expanded and occupied by large muscles (Fig. 34, B). In *Polycope* (Cladocopa) the two rami do not differ greatly in length. In the Podocopa only one ramus of three or four segments is well developed, and, according to the view of G. W. Müller, it is the *inner* ramus, the outer being represented by a small process tipped with setae or being altogether absent (Fig. 34, D). In *Cytherella* (Platycopa) the antenna differs from that of all other Ostracoda in having the peduncle divided into two segments and bent or geniculate between them (Fig. 34, C). The two rami are well developed—the inner, of three segments, resembling that of the Podocopa in the disposition of the sensory setae. The outer ramus has two segments. In the Cytheridae a large seta, bent at the tip, occupies the place of the vestigial outer ramus present in the other families of Podocopa. It serves as duct to a large unicellular gland. This was formerly regarded as a poison-apparatus, but, according to Müller, it is a spinning organ, by means of which the Ostracod covers with a network of fine threads the surface on which it is creeping, in order to obtain a secure foothold.

The *labrum* is usually well developed, and is especially large in Cypridinidae, where it contains a group of gland-cells. The *lower lip* is usually small, and only rarely shows traces of a division into paragnatha.

The *mandible* is characterised by the large size of the palp, which is often biramous and is sometimes pediform or variously modified. The gnathobase may be reduced to a small setose lobe (*Cypridina*), or to a curved serrated process extending into the gullet (*Asterope*). In *Sarsiella* it seems to be entirely absent, and the strong curved spines with which the tip of the palp is armed probably serve for seizing food and passing it into the mouth (Fig. 35, C). In the other families the gnathobase is usually well developed, and armed with spines and teeth. The palp usually consists of four segments, but the number is often reduced. In the Cypridinidae it is long and pediform, and is used in creeping. In *Sarsiella*, as already noted, it serves for the prehension of food,

and in the male of that genus it is apparently a clasping organ. In the Halocypridae (Fig. 35, B) and Polycopidae (Fig. 35, A) the first segment of the palp sends inwards a process tipped with spines, which lies alongside the gnathobase and assists in mastication. In *Cytherella* and some other genera the inner surface of the first and second segments of the palp bears a comb-like series

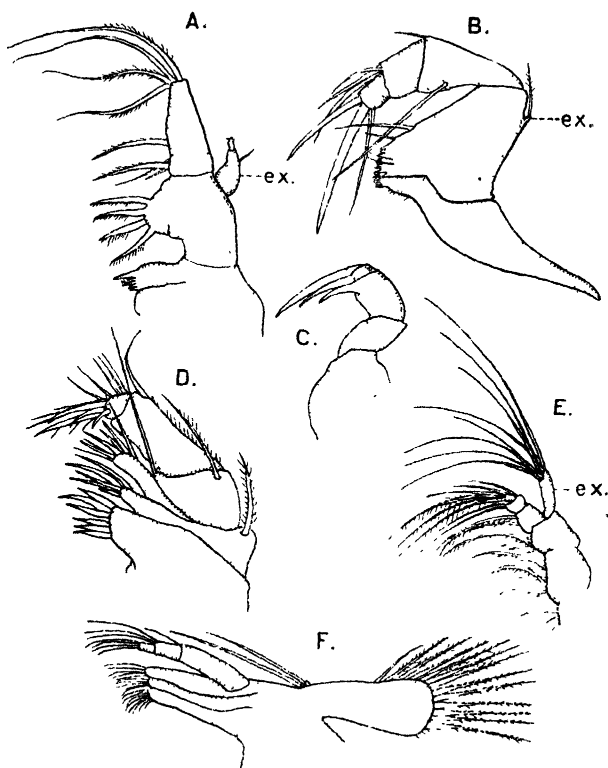


Fig. 35.

A, mandible of *Polycope frequens*. B, mandible of *Conchoecia magna*. C, mandible of *Sarsiella levis*, ♀. D, maxillula of *Philomedes interpuncta*. E, maxillula of *Polycopsis serrata*. F, maxillula of *Macrocypris succinea*. (After G. W. Muller.) *ex*, exopodite.

of long setae. The *exopodite* is represented in most Myodocopa by a small unsegmented appendage. In the Cyprididae and allied families it is a flattened plate with radiating fan-like setae or setiform processes, the so-called branchial appendage. In *Paradoxostoma* and some allied genera the mouth-parts are modified for piercing and sucking. The mandible is styliform, with a slender palp, and is enclosed in a conical beak formed by the labrum and hypostoma.

The structure of the *maxillula* varies very much in the different genera. The most primitive form is probably that found in the Cladocopa, where it consists of a protopodite of two segments, a three-segmented endopodite, and a small exopodite of one or two segments (Fig. 35, E). The segments of the protopodite are each produced inwards into a slight masticatory lobe. In the Halocypridae and most Cypridinidae (Fig. 35, D) the structure is similar, save that the exopodite is wanting. In most Podocopa the masticatory lobes are greatly produced, and the distal one is

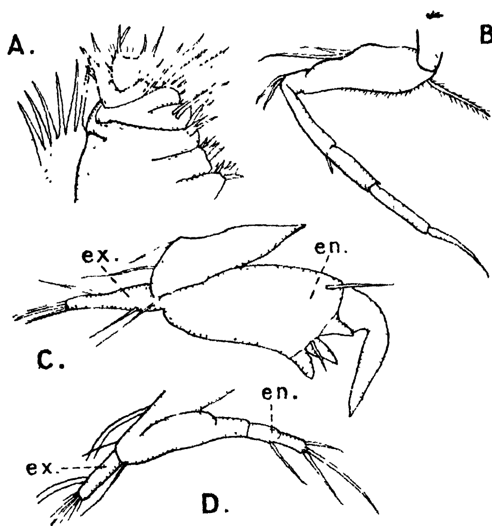


Fig. 36.

A, third post-oral appendage (so-called "second maxilla") of *Cypridina mediterranea* (young). B, third post-oral appendage (so-called "first leg") of *Cythereis convexa*. C, third post-oral appendage (so-called "maxilliped") of *Macrocypris succinea*, male. D, the same, female. (After G. W. Muller.) *en*, endopodite; *ex*, exopodite.

divided into two. The three segments of the endopodite may be distinct or may fuse into one. A large "branchial appendage," with radiating setae, may perhaps represent the exopodite (Fig. 35, F).

The *third post-oral limb* is of very diverse form, and has received different names in the various genera. Thus in the Cypridinidae it has been called the "second maxilla," in the Halocypridae and Cyprididae the "maxilliped," and in the Cytheridae and other families the "first leg." In the Cypridinidae it is quite maxilliform, and in the adult shows hardly any trace of segmentation. In young stages, however, Müller finds that it consists of six more or less distinct segments, of which two are assigned to the protopodite and the remainder to the endopodite (Fig. 36, A). A "branchial appendage" is present and is probably to be regarded

as the epipodite. In the other families the appendage is more leg-like. The "branchial plate" is commonly present, and sometimes an unsegmented appendage which is regarded as the exopodite. In many Cyprididae the limb forms, in the male, a strong clasping organ (Fig. 36, C), which may be unsymmetrically developed on the two sides. In *Cytherella* it has, in the male, much the same structure as in the Cyprididae, while in the female it is entirely absent. Finally, in the Bairdiidae and Cytheridae it is quite pediform (Fig. 36, B), with a strong terminal claw, and with or without a branchial plate.

The completely pediform character of this appendage in many Ostracoda suggests a doubt as to its homology with the maxilla of other Crustacea. This doubt is further strengthened by Müller's statement that the limb appears to belong to the thoracic rather than to the cephalic division of the body. More important still is the fact that in the course of development a pause in the successive appearance of the limbs occurs before this limb is added to the series. On these grounds there seems to be considerable probability in Müller's view that the maxilla has been entirely lost in the Ostracoda and that the appendage which occupies its place is to be regarded as homologous with the first thoracic appendage of other Crustacea.

In most Myodocopa the *fourth post-oral limb* is a maxilliform lobed plate, distinctly segmented only in *Cypridina* (Fig. 37, A). In *Sarsiella* and *Asterope* it is laminar and not lobed. In the Polycopidae it is absent. In the other families it is more or less leg-like (Fig. 37, B), with or without a branchial plate. In some Cytherellidae it forms a clasping organ in the male, while in the female it is reduced to the branchial plate.

In the Cytheridae, Bairdiidae, and Darwinulidae the *fifth post-oral limb* is pediform, with a strong terminal claw, and is used for creeping. In the Cyprididae (Fig. 37, D) it appears less adapted for locomotion, and is probably chiefly used as a "cleaning foot" for cleaning the other appendages and the inside of the shell. This is its only function in the Myodocopa (except Halocypridae), where it has a remarkable structure, being long and cirriform, divided into numerous segments moved by two muscles running along its whole length (Fig. 37, C). It is set high up on the side of the body, and the terminal part is armed with setae and chitinous teeth. In the Halocypridae the limb is greatly reduced and in the Cladocopa it is altogether absent.

A peculiar brush-like appendage found on the side of the body in the males of some Ostracods has been regarded as a vestigial sixth post-oral limb. It is found in a few Cyprididae and in *Cytherella* behind the last leg, and its position near the first leg (third post-oral) in the Bairdiidae and Cytheridae is explained as the result of a

secondary shifting of position. A similar organ has been found in one species of *Cypridina*.

It is not unlikely that at least one pair of limbs is involved in the composition of the penes of male Ostracods.

Alimentary System.—The oesophagus is narrow and has muscular walls. Its upper or posterior end projects into the capacious mid-

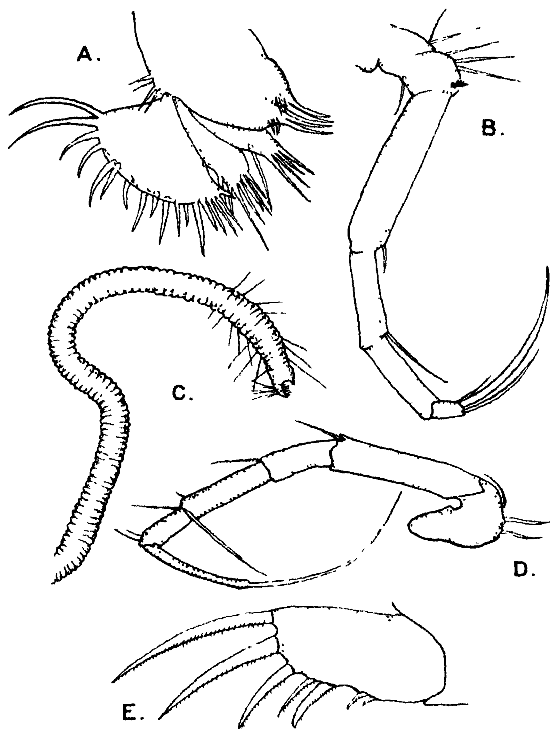


FIG. 37.

A, fourth post-oral appendage of *Cypridina mediterranea*. B, the same of *Macrocypris succinea*. C, fifth post-oral appendage of *Cypridina mediterranea*. D, the same of *Macrocypris succinea*. E, one ramus of the caudal furca of *Cypridina squamosa*, seen from the side. (After G. W. Muller.)

gut, and in the Podocopa is armed internally with chitinous ridges and teeth. In the Bairdiidae this apparatus is most fully developed and forms an efficient "gastric mill," moved by extrinsic and intrinsic muscles, for the trituration of the food.

The mid-gut in the Podocopa is divided into two parts by a constriction. Hepatic caeca may be absent as in *Cypridina*, numerous and small as in *Halocypris*, or large and reduced to a single pair which may extend into the shell-cavity, as in Cyprididae.

The short rectum opens on the ventral side of the furca in Myodocopa, but on the dorsal side in the Cyprididae and allied families.

Circulatory System.—A heart is present only in the Myodocopa (Fig. 38, *H*). It is placed near the dorsal surface just above the mandibles, and has one pair of lateral ostia and an opening in front through which the blood is expelled. No definite vessels exist, but a network of blood-channels is found in the shell of the Cypridinidae. The blood is coloured red in *Krithe*.

Respiratory System.—In the majority of Ostracoda the respiratory function is probably discharged by the general surface of the body and limbs and by the inner surface of the shell. The so-called "branchial appendages" found on the various limbs serve to keep up a current of water within the shell. Only in the genus *Asterope*, and less distinctly in one or two species of *Cypridina*, are definite branchiae found. These are lamellar appendages attached to the dorsal surface of the posterior part of the body. Seven pairs are present in *Asterope*.

Excretory System.—Little is known regarding the excretory system of the Ostracoda. "Segmental" organs in the form of small sacs lying at the bases of the ambulatory legs are described in *Paradoxostoma* and *Bairdia*. It is doubtful whether they open to the exterior. In *Cypris* a gland lying in the labrum and opening on the first segment of the antenna and a second gland opening on the basal segment of the third post-oral appendage (maxilla ?) have been described.

Glands.—As already stated, dermal glands are frequently found in the valves of the shell. In some Cypridinidae their secretion serves to agglutinate the sand in which these animals burrow, and in some cases to form definite tubular dwellings. In the Halocypridae the glands are most numerous near the edge of the anterior part of the shell, and it is stated that their mucus-like secretion serves to entangle food-particles and is then swallowed. Specially large glands opening near the margins of the valves anteriorly are found also in some other Ostracoda, and, from their position, suggest a comparison with the "fronto-lateral glands" similarly situated in the "Cypris-larva" of Cirripedes. Glands are sometimes found in the labrum (Cypridinidae and Cyprididae), and are believed, in *Pyrocypris*, to produce a luminous secretion. The spinning-glands of Cytheridae have already been mentioned.

Musculature.—The adductor muscle (Fig. 38, *S.M*) runs between the valves of the shell on the ventral side of the alimentary canal. In some Ostracoda, especially in Cyprididae, a tendinous plate is found below the anterior part of the alimentary canal, serving for the attachment of the mandibular and maxillary muscles. It is worthy of note that the adductor muscle does not share in its formation.

Nervous System.—The supraoesophageal ganglion is largest in the Cypridinidae in correlation with the presence of paired eyes in that family. The ventral nerve-chain is represented by a single

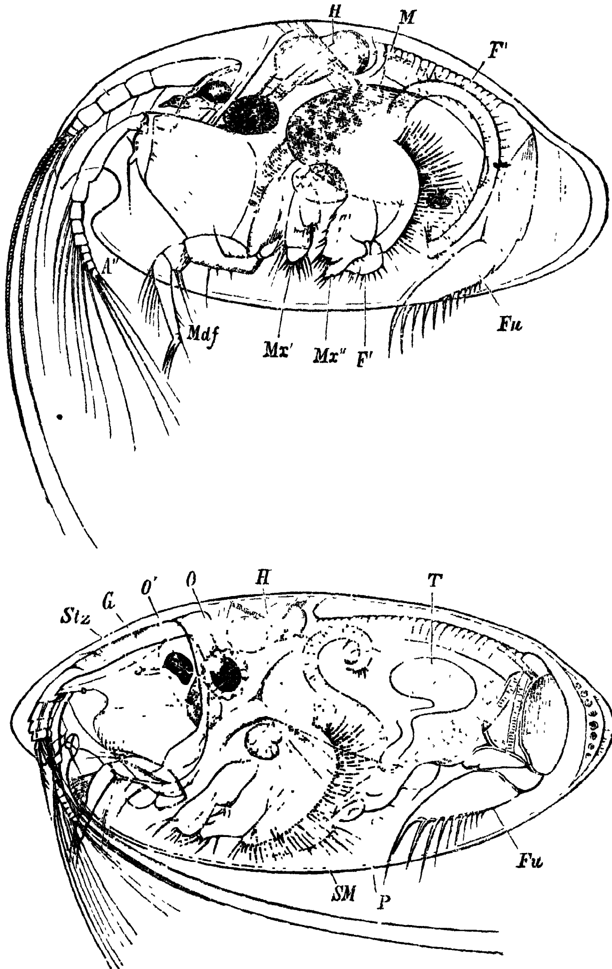


FIG. 38.

Cypridina mediterranea. Female (above) and male (below). One valve of shell removed to show appendages and internal organs. *A''*, antenna (the antennule is just above); *F'* (below), fourth post-oral limb; *F'* (above), fifth post-oral limb; *Fu*, caudal furca; *G*, brain; *H*, heart; *M*, mid-gut; *Mdf*, mandibular palp; *Mx'*, maxillula; *Mx''*, third post-oral limb (maxilla); *O*, paired eye; *O'*, median eye; *P*, penis; *S.M*, adductor muscle of shell; *Stz*, frontal tentacle; *T*, testis. (From Claus's *Textbook*.)

undivided mass in the Cyprididae, but in the Myodocopa it may be more or less completely divided into two or three (Halocypridae) ganglionic masses.

Sense-Organs.—Paired compound eyes are present only in the Myodocopa (excluding Halocypridae), where they project slightly from the surface of the head within the shell (Fig. 38, *O*). The number of ommatidia in each varies from four in *Sarsiella* to about fifty in some species of *Asterope*. The crystalline body in each is bipartite, and the rhabdom is longitudinally ribbed. There are no facets or cuticular lenses on the overlying cuticle, nor "eye-spots" on the shell. In *Philomedes* the eyes, though well developed in the male, are rudimentary in the female.

The nauplius eye is present in the majority of the Ostracods (Fig. 38, *O′*), and consists of the usual three pigment-cups containing each from 3 to about 100 retinal rods. In some Podocopa the three parts are widely separated from each other. A unicellular lens, or "crystalline body," is found in many Podocopa (Fig. 12, p. 18), and transparent "eye-spots" on the shell are common. In the Myodocopa the nauplius-eye lies at the base of a rod-like median process from the front of the head, the "frontal tentacle" (Fig. 38, *Stz*). Sometimes (Halocypridae) the distal portion of this tentacle is segmented off and is known as the "capitulum."

Olfactory filaments are present, commonly in greater numbers in the male than in the female, on antennules and antennae, and also on the "brush-like appendage."

Reproductive System: Female.—The ovaries are paired, and are generally lodged in the posterior part of the body. In the Cyprididae, and partly in the Cytheridae, they lie in the cavities of the shell-valves. The oviducts usually open separately behind the last pair of legs. In the Halocypridae the two oviducts unite shortly after leaving the ovaries, and the unpaired opening is situated on the left side just in front of the caudal furca. A *receptaculum seminis*, paired except in the Halocypridae, is always present. As a rule, it opens to the exterior by a special copulatory pore, and communicates internally with the oviduct, but sometimes only the external opening appears to be present, while in the Cyprididae the opening into the oviduct serves both for entrance and exit.

Male.—The testes are simple in the Myodocopa (Fig. 38, *T*), four-lobed in most of the other families. In the Cypridinidae the two *vasa deferentia* unite to open by a single median pore lying between the paired penes, which in this family alone are not traversed by the ducts (Fig. 38, *P*). In the Halocypridae the penis is unpaired and lies to the right of the middle line. The vasa deferentia unite just before entering it. In the other families

the vasa deferentia are probably always united by a transverse duct shortly after leaving the testes. They are often of great length and are coiled in a very complex fashion, differing in the different groups. The distal part forms a *ductus ejaculatorius* of complicated structure, with muscular walls. The paired penes are traversed by the vasa deferentia, the terminal portion forming a protrusible copulatory tube, and the penis is often armed with chitinous hooks moved by special muscles.

The spermatozoa are sometimes spherical (*Asterope*), more commonly filiform. In the Cyprididae they are of a size which relatively, if not absolutely, is unique in the animal kingdom. In *Pontocypris monstrosa* the total length of the animal is ·6 mm., while the spermatozoa are 5·0-7·0 mm. long.

Development.

The eggs are carried within the valves of the shell dorsally to the body of the animal in the Cypridinidae, Cytherellidae, some Cytheridae, and in the freshwater genus *Darwinula*, and in a few cases the young are carried for some time after hatching. In other cases the eggs are deposited on water-plants or shed free in the water. The course of development is best known in the Cyprididae. On hatching, the larva is already enclosed within a bivalve shell, but otherwise corresponds in structure to a nauplius (Fig. 39). Three pairs of appendages are present, antennules, antennae, and mandibles, the last two, however, not distinctly biramous. In the Cytheridae the mandible at this stage is rudimentary. The remaining limbs are added at successive moults in regular order from before backwards. According to Müller, it is not the case that, as stated by Claus, the fourth post-oral limbs appear before the third. There is, however, a marked pause in the development before the appearance of the third post-oral pair, and this, as already pointed out, supports the view that a pair of appendages corresponding to the maxillae of other Crustacea is missing.

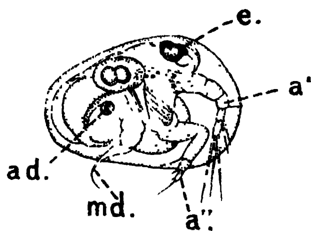


Fig. 39.

Nauplius stage of *Cypris*. *a'*, antennule; *a''*, antenna; *ad*, adductor muscle of carapace; *e*, nauplius eye; *md*, mandible. (After Claus.)

Remarks on Habits, etc.

The Ostracoda are abundant both in fresh waters and in the sea, generally burrowing in mud or creeping among weeds. The marine Halocypridae belong to the plankton. None are definitely

known to be parasitic, but one species found in the gill-chambers of Crayfish in North America may be so. The majority are minute, very many not exceeding 0·5 mm. in length. The Myodocopa are usually larger than the Podocopa, many being 1 or 2 mm. long. The largest known Ostracod, a species of *Gigantocypris*, is 23 mm. in length.

PALAEONTOLOGY.

Fossil Ostracoda are abundant in all geological formations from the oldest to the most recent, but, with hardly an exception, only the shell is preserved and the affinities of the numerous genera which have been established remain quite uncertain. Most of the Ostracoda from Cambrian rocks belong to the genera *Primitia*, Jones, and *Leperditia*, Rouault, while *Beyrichia*, M'Coy, is common in the Silurian. Species referred to the recent genus *Cypridina* occur in the Carboniferous, and *Cythere* and other recent genera are stated to make their appearance in the Permian.

AFFINITIES AND CLASSIFICATION.

In the bivalved form of the shell, the ventrally flexed posterior part of the body, the form of the caudal furca (in the Myodocopa), and the biramous natatory antennae (especially of the Cladocopa and Platycopa), the Ostracoda present important resemblances to the Conchostraca and Cladocera among the Branchiopoda. There might, indeed, be little difficulty in regarding them as derived from the Conchostraca, were it not for the presence of the mandibular palp, which is absent from the Branchiopoda. The possession of this appendage and its biramous form in many cases point to the origin of the Ostracoda as an independent branch of the primitive Crustacean stock. There appears to be no reason, however, to suggest, as Claus has done, that the small number of appendages is a primitive character.

In the possession of paired eyes and a heart, the Cypridinidae are more primitive than the other Ostracoda, although in the form of the antennae and in some other points they are probably more specialised than the Cladocopa and Platycopa.

The classification given below is that of Sars, as modified by Brady and Norman. In the more recent arrangement of G. W. Müller the Cladocopa are included in the Myodocopa and the Platycopa in the Podocopa, and the number of families is considerably reduced.

SUB-CLASS OSTRACODA.

ORDER 1. **Myodocopa.**

Shell generally with antennal notch; antennae with massive basal segment, generally biramous, exopodite generally with eight or nine

segments, endopodite minute and generally prehensile in male ; five pairs of post-oral limbs ; caudal furca with lamellar rami armed with spines.

Family HALOCYPRIDAE (CONCHOECIIDAE). *Halocypris*, Dana ; *Conchoecia*, Dana. Family ASTEROPIDAE. *Asterope*, Philippi (= *Cylindroleberis*, Brady). Family CYPRIDINIDAE. *Cypridina*, H. Milne-Edwards ; *Philomedes*, Lilljeborg (Fig. 33, A) ; *Pyrocypris*, G. W. Muller ; *Gigantocypris*, G. W. Muller. Family RUTIDERMATIDAE. *Rutiderma*, Brady and Norman. Family SARSIELLIDAE. *Sarsiella*, Norman.

ORDER 2. **Cladocopa.**

Shell without antennal notch ; antennae biramous, both rami well developed and natatory ; only three pairs of post-oral limbs ; other characters as in Myodocopa.

Family POLYCOPIDAE. *Polycope*, G. O. Sars ; *Polycopsis*, G. W. Müller.

ORDER 3. **Podocopa.**

Shell without antennal notch ; antennae with basal segment not enlarged, one ramus (exopodite, Muller) vestigial or absent, the other of not more than four segments ; five pairs of post-oral limbs ; caudal furca with styliform or vestigial rami.

Family PARADOXOSTOMATIDAE. *Paradoxostoma*, Fischer. Family CYTHERIDAE. *Cythere*, O. F. Muller ; *Cythereis*, G. O. Sars (Fig. 33, C) ; *Krithe*, Brady. Family DARWINULIDAE. *Darwinula*, Brady and Robertson. Family BAIRDIIDAE. *Bairdia*, M'Coy. Family CYPRIDIDAE. *Cypris*, O. F. Muller (Fig. 33, B) ; *Pontocypris*, G. O. Sars. Family CYPRIDOPSIDAE. *Cypridopsis*, Brady.

ORDER 4. **Platycopa.**

Antennae biramous, protopodite of two segments, endopodite of three, and exopodite of two segments ; only four pairs of post-oral limbs ; other characters as in Podocopa.

Family CYTHERELLIDAE. *Cytherella*, Bosquet.

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CHAPTER IV

THE COPEPODA

SUB-CLASS COPEPODA, H. Milne-Edwards (1830).

Order 1. **Eucopepoda.**
 Sub-Order 1. **Gymnoplea.**
  Tribe 1. Amphaskandria.
  „ 2. Heterarthrandria.
 Sub-Order 2. **Podoplea.**
  Tribe 1. Isokerandria.
  „ 2. Ampharthrandria.
Order 2. **Branchiura.**

Definition.—Crustacea in which there is no distinct shell-fold, though the dorsal shield of the cephalon may be enlarged by the coalescence of one or more of the trunk-somites; there are typically nine free trunk-somites (besides the telson), the last four without appendages; the telson bears a caudal furca; the antennules and antennae are generally large, the latter sometimes biramous, and both may be used for locomotion or for prehension; the mandibles may have a palp, sometimes biramous; there are typically six pairs of trunk-limbs, the last five biramous and natatory, but the sixth pair are frequently reduced or absent; the genital apertures are on the seventh trunk-somite (except in Branchiura); the paired eyes are absent (except in Branchiura); development with metamorphosis, the young generally hatched in nauplius stage. (Most of these characters are subject to modification in parasitic forms.)

Historical.—The relatively large size attained by some of the parasitic Copepoda renders it probable that they were the first to attract attention, and it is possible, though not certain, that they are referred to in certain passages of Aristotle. The minute free-living forms remained unnoticed till some of the microscopists of the seventeenth century—notably Leeuwenhoek—described and figured the common freshwater *Cyclops*. It was long, however,

before the affinity of the two groups was recognised. Linnaeus included some free-living Copepods in his genus *Monoculus*, among the Crustacea, but some of the parasites were placed under "Vermes mollusca" in the genus *Lernaea*, and others among the "Zoophyta" in the genus *Pennatula*. O. F. Müller's great work on the "Entomostraca" marks the beginning of a new epoch in the study of the group. The genera *Cyclops*, *Caligus*, and *Argulus* were established by Müller, besides two others based on larval stages, one of which, the *Nauplius*, still bears the name given to it by Müller. Jurine's *Histoire des Monocles* (1820) is noteworthy, among much else, for the description of the larval metamorphosis of *Cyclops*, the earlier stages of which had been seen long before by Leeuwenhoek and de Geer. Although an affinity between the highly modified Lernaeidae and the less-specialised parasites like *Caligus* was suggested, more or less definitely, by Oken, Lamarck, and others, it was not until von Nordmann's researches (1832) threw light on their development that the Lernaeidae and their allies were definitely accepted as Crustacea. In most systems of classification, however, the parasites were more or less widely separated from the free-living forms, and by Milne-Edwards they were even placed alongside of the Pycnogonida in a different sub-class. Milne-Edwards introduced the name Copepoda for the free-living forms alone. Zenker, in 1854, seems to have been the first to associate together free-living and parasitic forms under the name Entomostraca. Modern conceptions of the morphology and classification of the Copepoda are largely based upon the long series of highly important memoirs (1857-1895) by C. Claus. Among faunistic workers, J. D. Dana, H. Kröyer, Steenstrup and Lütken, van Beneden, and Brady, may be specially mentioned. In more recent years, W. Giesbrecht, in his splendid monograph of the pelagic Copepoda and other important works, has given a new aspect to the problem of classification, by showing that the parasitic habit has been acquired not once but many times in the evolution of the group, and that the line of division, maintained even in Claus's classification, between free-living and parasitic forms must be abandoned. Hansen's fine monograph of the Choniostomatidae has raised that family, previously obscure, to the position of one of the best known among the parasitic groups. Finally, G. O. Sars's work on the Copepoda of Norway, now in course of publication, is especially important as regards the bottom-living marine forms, which in recent years have been less studied than the more easily collected pelagic species. The small group of the Branchiura, associated by the older authors with the parasitic Copepoda, were removed by Zenker to the Branchiopoda. Claus restored them to the Copepoda, and his arrangement is followed here, but in view of the important differences which separate them

from the Eucopepoda, it will be more convenient to deal separately with the morphology of the two groups.

Morphology of Eucopepoda.

Apart from the parasitic forms, which exhibit an endless variety of modifications, the Eucopepoda present a considerable uniformity in general shape. The body is divided into two regions, of which the anterior is sub-cylindrical or flattened, and is more or less sharply marked off from the posterior region, which is usually much narrower and terminates in a well-marked caudal furca. There are typically ten free segments (including the telson) behind the head, and the limit between the two regions is marked by a very movable articulation which falls either between the fifth and sixth of these (Gymnoplea) or between the fourth and fifth (Podoplea) (Fig. 40). Giesbrecht has suggested that the limit between these regions is really in the same position in both cases, that the fifth thoracic somite of the Gymnoplea is unrepresented in the Podoplea, and that the so-called fifth thoracic somite of the last-named group is a "pre-genital" somite which is suppressed in the Gymnoplea. The evidence in favour of this view, however, is very slight. The head-region is usually stated to include, in addition to the primitive cephalic somites, that corresponding to the maxillipeds or first post-maxillary appendages. It appears, however, that in some larvae the line of articulation defining the first free somite runs in front of the maxillipeds, and it is possible that the somite bearing these appendages should be regarded as coalesced not with the head-region but with the following somite. The next five somites bear swimming-feet, and constitute what is commonly called the thoracic region. It seems advisable, however, to extend the meaning of the term *thorax* to include also the somite of the maxillipeds. The remaining

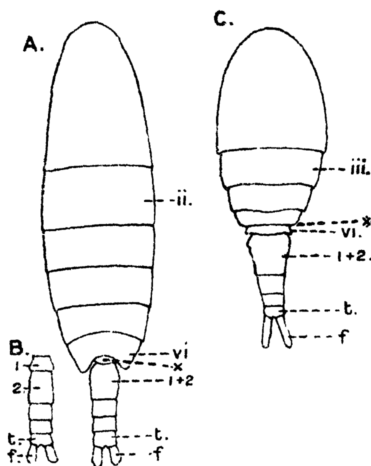


Fig. 40.

Segmentation of the body in Gymnoplea and Podoplea. A, outline of the body of female *Calanus* (Gymnoplea), dorsal view. B, abdomen of male *Calanus*. C, outline of female *Cyclops* (Podoplea). ii, iii, vi, second, third, and sixth thoracic somites (commonly reckoned as first, second, and fifth respectively); 1+2, first and second abdominal somites, coalesced in the female sex in both instances; *t*, telson; *f*, caudal furca. * marks the position of the movable articulation between the anterior and posterior divisions of the body.

four somites with the telson constitute the *abdomen*, and are limbless, with the possible exception of the first or genital somite, which bears, in both sexes, the external openings of the genital organs, and may have what are sometimes regarded as the vestiges of a pair of appendages.

In the majority of cases the number of free somites is reduced by coalescence. Very often the second (commonly reckoned as the first) thoracic somite, bearing the first pair of swimming-feet, is fused with the head, and not infrequently (in the Gymnoplea) the

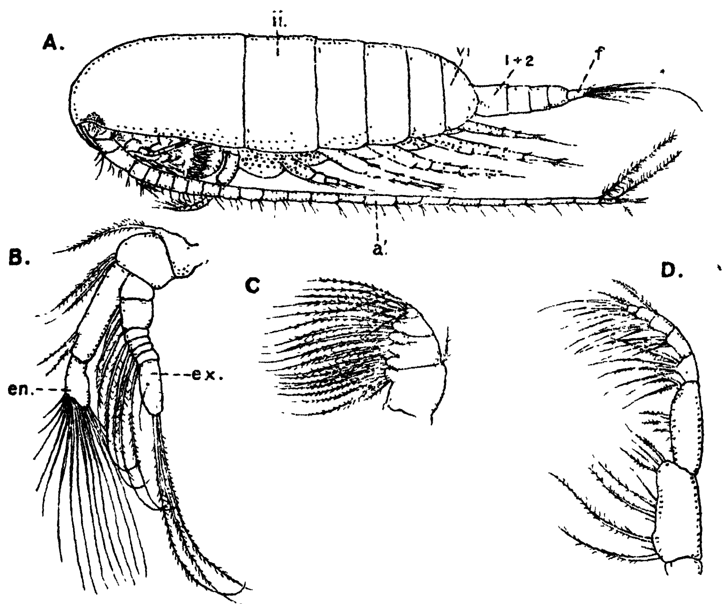


FIG. 41.

A, *Calanus finmarchicus*, female, from the side, × 16; B, antenna; C, maxilla; D, maxilliped. ii and vi, second and sixth thoracic somites; 1+2, first and second abdominal somites coalesced; *a'*, antennule; *en*, endopodite; *ex*, exopodite; *f*, caudal furca. (After Sars.)

last two thoracic somites fuse together. The abdominal somites are usually all distinct in the male sex (Fig. 40, B), but in the female this is rarely the case, the first two being generally fused (Figs. 40 and 41, A), and the number may be still further reduced.

While there is no distinct shell-fold, the head-region usually possesses more or less well-developed pleural folds, which may be directed downwards or even inwards so as partially to enclose the bases of the limbs. These pleural folds are repeated on the free thoracic somites, but are as a rule absent on the abdomen. Anteriorly the tergal plate of the head-region is often produced into a rostral process which may be a flattened plate, movably articu-

lated with the head in some Harpacticidae, and resembling the rostral plate of the Leptostraca. More usually the rostrum is bent down under the head and is often forked. A very remarkable modification of the rostrum found in some Pontellidae is mentioned below in connection with the eye.

The two rami of the *caudal furca* are usually movably articulated with the telson or terminal segment. Their setae are very constant in number and position, and afford valuable systematic characters. In some pelagic forms these setae attain an exaggerated development (Fig. 42), while in some commensal or parasitic forms they become converted into hook-like organs of adhesion (*Doropygus*). Between the furcal rami and somewhat on the dorsal side is the anal aperture, covered by a small supra-anal

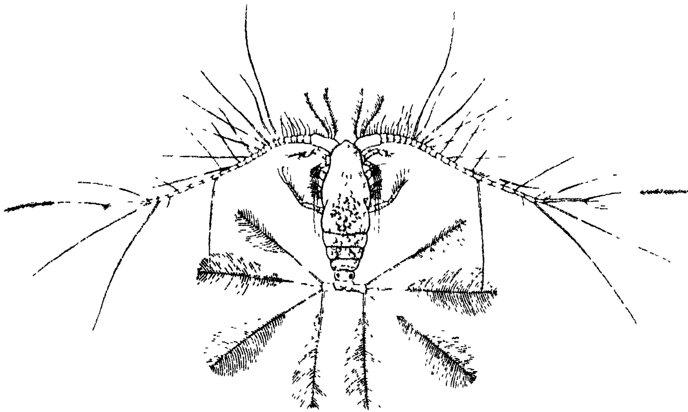


FIG. 42.
Calocalanus pavo, × 16 (After Giesbrecht.)

plate which may represent the post-anal region of the telson in the Branchiopod *Lepidurus* and the Malacostraca.

A modification of the thoracic region which may be mentioned here is the development in several Ascidicolidae of a dorsal brood-pouch formed by a fold of the integument arising sometimes from the fourth, sometimes from the second free thoracic somite.

The modifications which the form of the body undergoes in parasitic Eucopepoda consist in the coalescence of somites leading ultimately to the disappearance of segmentation, and in the development of lobes and processes from the various regions of the body. The free edges of the thoracic somites may be produced into lamellar appendages, or wing-like lobes may be developed on the dorsal surface (*Notopterophorus*).

Appendages.—The *antennules* are always uniramous, and in many

of the free-living Eucopepoda they assist in swimming. They are further modified in many cases, in the male sex, to act as prehensile organs for seizing the female. They are most fully developed in the Gymnoplea, where they may exceed the body in length and may consist of twenty-five segments (Fig. 41, A, *a'*). Throughout the Gymnoplea and also in the Cyclopidae and Asterocheridae, where the number of segments is less, Claus and Giesbrecht have demonstrated their homology with those of the twenty-five-segmented form. As an example we may give Giesbrecht's comparison of the segmentation of the antennules in a species of *Cyclops*, with the typical arrangement as found in many Gymnoplea.

Gymnoplea	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25
Cyclops ♂	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17
Cyclops ♀	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17

In the Harpacticidae and other families with a reduced number of segments the homology has not been demonstrated, but there can be little doubt that the twenty-five segments of the Gymnoplea represent the typical and primitive arrangement from which the others have been derived. In the parasitic forms the antennules are usually greatly reduced. In the Caligidae the basal portions of the antennules become coalesced with the front of the head, forming a bilobed prominence. In some genera this bears, on either side, a sucker which serves to attach the parasite to its host. Except in this instance, however, the antennules do not become converted into organs of attachment as the antennae frequently do.

In most, perhaps in all cases, the antennule, as in other Crustacea, bears sensory setae of the type to which Giesbrecht has given the name "aesthetases," and these are commonly more numerous in the male sex. In some cases each antennule bears only a single aesthetase, which may then be of relatively great size.

In those Eucopepoda in which the antennule of the male is transformed into a clasping organ for seizing the female, the distal is flexed upon the proximal portion (Fig. 43, A). It is probable that the point at which this flexion takes place is the same in all cases, corresponding to the articulation between the eighteenth and nineteenth of the primitive series of segments. The proximal portion of the appendage becomes more or less swollen, owing to the strong development of flexor and extensor muscles of this joint, and the opposed edges are often armed with teeth or spines. In those Gymnoplea in which this clasping apparatus is developed, only one, generally the right, antennule is modified (Heterarthrandria). In the Podoplea, on the other hand, the modification, when present, is bilateral. The occurrence of this modification of the male antennules in many families of Eucopepoda which, in any

scheme of classification, are widely separate from each other, and especially the fact that the geniculation occurs in the same place in some, probably in all cases, suggests that this character is a primitive one for the whole group, and that its absence is a secondary modification. This view is supported by the interesting fact observed by Claus, that in some Gymnoplea Amphaskandria a trace of this modification persists in the coalescence of the twentieth and twenty-first segments of the antennule in the male,

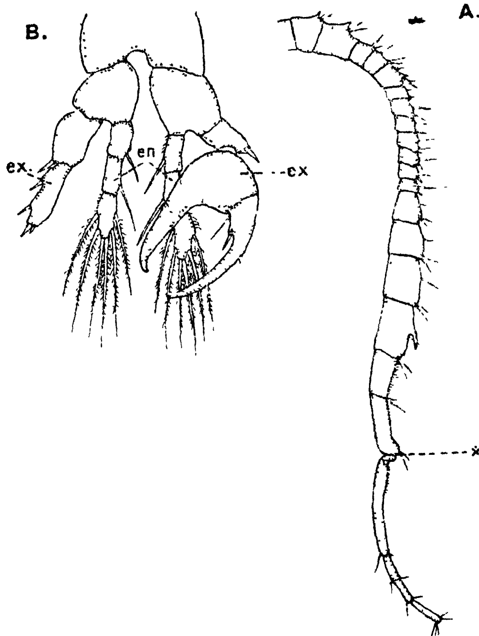


FIG. 43.

A, clasping antennule of male [illegible] (Gymnoplea, Heterarthrandria), *, position of the hinge-joint. B, last pair of thoracic limbs of the same. *en*, endopodites; *ex*, exopodites, that of the right side modified as a chelate grasping organ. (After Sars.)

and that in some cases this coalescence only appears in the antennule of one side as in the allied Heterarthrandria.

The *antennae*, like the antennules, preserve in many Eucopepoda the general structure and the natatory function which they have in the nauplius. They are most fully developed in the Gymnoplea, where they consist of a protopodite of two segments, an endopodite of two segments, and a multi-articulate exopodite, and bear numerous long natatory setae (Fig. 41, B). In the Podoplea the natatory function is less well marked,

being usually superseded by that of clinging organs. In the Harpacticidae and Asterocheridae the exopodite is retained, though often reduced to a single segment. In the other families it disappears altogether. The endopodite never consists of more than two segments, so that in the absence of the exopodite the appendage is usually composed of four segments. In the parasitic families the antennae generally form organs for attachment to the host, provided with a strong curved claw and, in some cases, even with a chelate termination.

The *labrum* and *metastoma* are very variously modified, especially in the parasitic forms, and will be described below in connection with the other mouth-parts. In the free-living forms the metastoma may either form a simple ridge or may be provided with a pair of movable lateral lappets.

The *mandibles* are especially interesting from the fact that in many Eucopepoda (especially the Gymnoplea) they retain more completely than in any other Crustacea the form of biramous swimming-limbs which they possess in the nauplius. The body of the mandible is formed by the proximal segment, and the remainder of the protopodite, together with the endopodite and exopodite, forms the "palp" (Fig. 8, A, p. 12). Hansen has pointed out the existence in some Gymnoplea of a minute intermediate segment between the body of the mandible and the large segment which bears the endopodite and exopodite. It would seem, therefore, that the body of the mandible in the Eucopepoda, and no doubt also in other Crustacea, represents the precoxal segment of the limb. The endopodite, as in the case of the antennules, consists of, at most, two segments, while the exopodite may consist of five or six. The cutting edge in most free-living forms is armed with teeth and setae.

The type of mandible just described is universal among the Gymnoplea and is found in some Harpacticidae and Ascidicolidae. More usually, however, among the Podoplea the palp is reduced, as in *Cyclops*, to a papilla bearing a tuft of setae, or is altogether absent. The form of the cutting edge is variously modified, especially in the parasitic and semiparasitic forms. In many of these the mandibles have a sickle-shaped blade, with the point directed into the cavity of the mouth, but in those forms which have completely suctorial mouth-parts (formerly grouped together as Siphonostomata) the mandibles become simple piercing stylets, and are enclosed within a conical or tubular "siphon" formed by the upper and lower lips. In some cases the siphon may be as long as the body (*Acontiophorus*) (Fig. 44, A). The structure of this siphon is not in all cases the same, though it does not seem to be the case, as has been stated, that it is ever formed from the labrum alone.

The *maxillulae* (commonly called the maxillae) are most com-

pletely developed in the Gymnoplea and some Harpacticidae, in which endopodite, exopodite, and epipodite are distinct, and the protopodite is produced internally into a large masticatory lobe and two smaller distal lobes (Fig. 9, A, p. 13). In the Cyclopidae the epipodite has vanished, the exopodite and endopodite are very small, and only the large masticatory process of the protopodite persists. In many Harpacticidae and in the other families the maxillula undergoes various degrees of reduction.

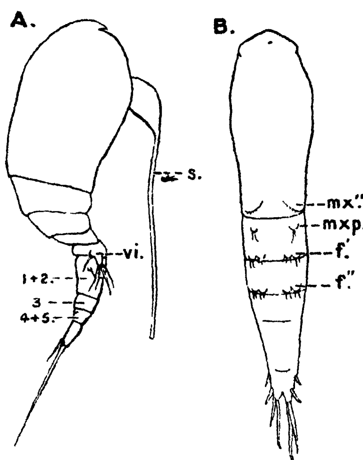


Fig. 44.

A, *Acontiophorus scutatus*, ♀, from the side, × 50. Most of the appendages are omitted. *s*, suctorial siphon; *vi*, the rudimentary sixth pair of thoracic limbs; 1+2, the coalesced first and second abdominal somites; 4+5, the fourth abdominal somite coalesced with the telson. (After Giesbrecht.) B, larva of *Rhincalanus nasutus* in last metanauplius stage. The outline of the body as seen from above. The first three pairs of appendages are omitted, but the rudiments of the posterior appendages are seen by transparency through the body. *mx*", maxillae; *mxp*, maxillipeds separated from the maxillae by the line defining the first thoracic somite; *f'*, *f"*, first and second pairs of swimming-feet. (After Giesbrecht.)

The two pairs of appendages succeeding the maxillulae are commonly designated the outer (or anterior) and inner (or posterior) maxillipeds, and were for long considered to represent the separated rami of a single pair of appendages. This interpretation was put forward by Claus, who found that, in the metanauplius stage of *Cyclops* and other forms, the two appeared to arise from a single rudiment. Hansen, however, has discovered, and the observation has been confirmed by Giesbrecht and by Claus himself, that in the larvae of certain marine Gymnoplea (*Eucalanus*, *Rhincalanus*, *Pontella*, etc.) in which the body is more elongated than usual, the rudiments of the two appendages are not only quite distinct, but are separated from each other by the suture line which marks off from the head the so-called first thoracic somite (Fig. 44, B). The "outer (or anterior) maxillipeds" are therefore the *maxillae*, while the inner (or posterior) pair, for which the name *maxillipeds* may be retained, must be regarded as the first of the thoracic series, and the somite corresponding to them is, at least in some cases, coalesced with that which bears the first pair of swimming-feet. The maxilla in its most fully developed form consists of a flattened and shortened axis of, at most, eight segments, of which the first and second each bear two, and the third a single endite (Fig. 41, C). In the Gymnoplea this appendage is beset with plumose setae, which act as a net in collecting food-

particles. In the Podoplea the setae are generally much reduced, and stout spines are developed on the endites. In many cases, especially in parasites, the armature is reduced to a single terminal claw-like spine and the limb is exclusively a clinging organ.

In the parasitic family Lernaeopodidae, a very remarkable apparatus of attachment is formed by two appendages which unite to form a sucker-like organ of complicated structure (Fig. 45, B). In some cases, when the appendages are short, they coalesce completely to the base, but in other cases they have the form of

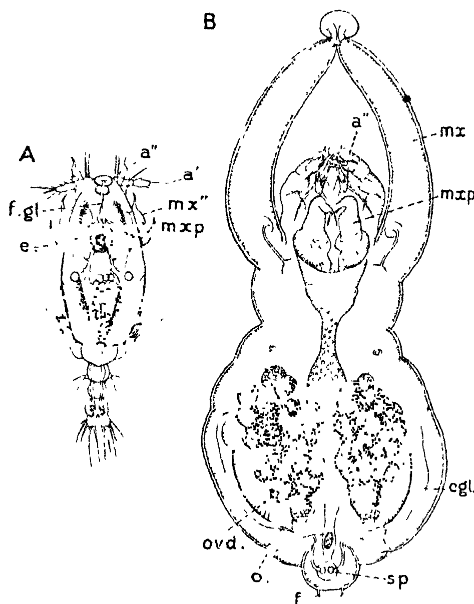


Fig. 45.

Achtheres percarum (Lernaeopodidae). A, larva in first Copepodid stage, dorsal view. B, adult female, ventral view, × 25. *a'*, antennule; *a"*, antenna; *c.gl*, cement gland opening into oviduct; *e*, median eye; *f*, caudal furca; *f.gl*, frontal cement gland; *mx"*, maxilla; *mxp*, maxilliped; *o*, opening of oviduct; *ovd*, oviduct distended with eggs; *sp*, openings of spermathecae. (After Claus, slightly modified.)

long arms, united only at the tip. These appendages have been regarded sometimes as the "first maxillipeds" (maxillae) and sometimes as the "second maxillipeds" (here called maxillipeds). The fact that a pair of glands, identified as the maxillary (excretory) glands, open at their base, seems to show that the former interpretation is the correct one. An apical coalescence of paired appendages is not known to occur in any other Arthropods.

The *maxilliped* (first thoracic limb) is always uniramous, and is generally more elongated than the maxilla (Fig. 41, D). It consists

of, at most, seven (perhaps eight) segments, but the number is often much reduced, and, as in the case of the maxilla, the limb is commonly modified into a clinging organ with a strong terminal claw, or, as in a section of the Harpacticidae, into a subchelate, prehensile "hand."

The five following pairs of appendages (the thoracic limbs of the ordinary terminology, the second to the sixth of the system here adopted) are in some Gymnoplea all similar and in the form of biramous swimming-legs. This form is retained by some, at least, of these limbs in all Copepoda in the later larval if not in the adult stage, and constitutes one of the most general characters of the sub-class.

Each consists typically of a broad and flattened protopodite of two segments, and of an endopodite and exopodite, each with, at most, three segments, flattened, and bearing marginal natatory setae together with, on the outer edges, strong spines (Fig. 3, B, p. 8). The proximal segments of the protopodites of each pair are connected with each other across the middle line by a plate formed by a transverse fold of the sternal integument (the "Bauchwirbel" of Zenker), so that in the backward and forward movement in swimming the two appendages move as one.

The last (sixth) pair of thoracic limbs are similar to the preceding pairs only in the females of some genera of Gymnoplea. In the male sex of that order they are always modified into copulatory organs, often very complex, by means of which the spermatophores are affixed to the copulatory aperture of the female. This modification is asymmetrical on the two sides in correlation with the asymmetrical development of the internal generative organs in the group (Fig. 43, B). In the females of many Gymnoplea the appendages exhibit every stage of reduction even to complete disappearance. In the Podoplea the appendages are always present (Fig. 44, A, vi.), except in the more degraded parasites; always vestigial, consisting of one or two small segments; and are not specially modified in the male. In some Harpacticidae and Ascidicolidae, however, they become enlarged in the female sex into plate-like appendages serving to protect the egg-masses. It is noteworthy that these vestigial limbs of the last pair may persist even in cases where the preceding pair of limbs is suppressed.

In the Podoplea (but not in Gymnoplea) the genital apertures of the female on the first abdominal somite are guarded by valvular plates moved by muscles. These valves have been supposed to represent a vestigial pair of appendages.

In the parasitic forms, with the loss of the power of locomotion, the thoracic limbs become more or less reduced. In *Lernaeocera*, for example, they persist as microscopic though completely formed limbs set at long intervals along the length of the unsegmented

body. In the Chondracanthidae the anterior two pairs alone are developed, and these become enlarged in the adult into clumsy, unsegmented bifid lobes. In other cases the thoracic limbs are reduced to minute, unsegmented processes, or some or all of them may disappear. In a few cases the adult is entirely without appendages, as in the Herpyllobiidae.

Alimentary System.—The alimentary canal is in many cases of simple form, not divided into sharply defined regions and without diverticula. The stomodaeum and proctodaeum are short. In many Gymnoplea there is a short median diverticulum anteriorly, and in some cases, immediately behind this, a pair of small lateral (hepatic) caeca which may be bifid (*Eucalanus*). In some Corycaeidae and Asterocheridae these caeca are large and much branched (Fig. 46). Groups of gland-cells described as salivary occur in the region of the labrum and epistome.

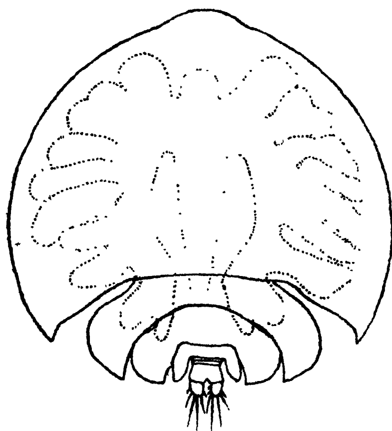


FIG. 46.

Artotrogus orbicularis. Outline of body, from above, showing ramified lateral diverticula of the alimentary canal. (After Giesbrecht.)

The extrinsic muscles of the alimentary tract are well developed in Eucopepoda. Certain muscles running from the anterior part of the gut to the dorsal and anterior region of the body-wall are of importance in producing a rhythmical displacement of the whole alimentary canal, and serving, in the absence of a heart, to cause a circulatory movement of the blood. In some parasites the dilator muscles of the oesophageal region are greatly developed and act as a suctorial apparatus. The short rectum (proctodaeum) is usually provided with dilator muscles running outwards to the body-wall in addition to the usual constrictors, and the rhythmical movements of dilatation and contraction produced by them have been regarded as subservient to a process of anal respiration.

The alimentary canal is usually nearly straight (except for the sternal flexure of the oesophageal portion), but in a few Gymnoplea and in *Cancerilla* (Asterocheridae) its course is slightly sinuous.

Circulatory System.—A heart is present in most Gymnoplea and in the genus *Misophria* among the Podoplea. In all other Copepoda it appears to be wanting. When present it has an abbreviated saccular form, and is situated in the region of the first or second

free somite. There are three ostia, one median on the posterior surface and a lateral pair. Anteriorly the heart gives off an aortic vessel, usually very short. Only in *Eucalanus* is the aorta described as extending into the frontal region of the head and dividing into two pairs of lateral vessels.

In the majority of the free-living Podoplea where the heart is absent the blood is kept in motion mainly by the continuous rhythmical backward and forward movements of the alimentary canal, effected by the extrinsic muscles already mentioned. In certain parasitic forms (*Caligus*, young *Achtheres*) a heart, or an apparatus having an analogous function, is said to be present, but exact details as to its structure are wanting.

In *Lernanthropus* and some other Dichelestiidae a closed system of vessels is present containing a yellowish or reddish fluid. There is no heart, and the relation of this system to the circulatory apparatus of other Copepoda is quite obscure.

Excretory System.—The maxillary ("shell") gland is the functional excretory organ in the adult stage of most, if not all, Copepoda. It is much larger in the freshwater forms, where the duct is long and convoluted, than in the marine forms, in which it is often hard to find, and sometimes apparently absent. The end sac is small, and the tube terminates in a short chitin-lined duct opening on the posterior surface of the maxilla.

In the freshwater Harpacticid *Belisarius* a curious vibratile organ is found connected with, or in close proximity to, the maxillary gland. It has been supposed to be of the nature of a "flame-cell," but it is more probably a muscular fibre or membrane aiding the circulation of the blood in the neighbourhood of the gland.

Glands.—Unicellular dermal glands are present on the body and limbs of most Eucopepoda. Certain pelagic forms belonging to various genera of the Centropagidae and Oncaeidae are known to be phosphorescent, and Giesbrecht has shown that this is due to certain of the dermal glands, the secretion of which becomes luminous on issuing from the apertures of the glands. In freshwater Cyclopidae and Harpacticidae the secretion of the dermal glands envelops the body when the water dries up, and forms a protective case enabling the animal to survive prolonged desiccation.

Nervous System.—The ventral nerve-cord is always short, not reaching beyond the fourth free thoracic somite. It is divided into distinct ganglia in the Gymnoplea, but in the Podoplea, so far as is known, the ganglia are all coalesced. In the Corycaeidae and in the parasitic families the whole system is still more concentrated, forming a thick perioesophageal ring. Even in the Gymnoplea the distinction between ganglia and commissures is not sharp, nerve-cells being present abundantly on the latter as on the former.

In *Cyclops* it has been observed that the pair of nerves to the antennae originate from the oesophageal connectives, so that as regards their nerve-supply these appendages are parastomial.

Sense-Organs.—The paired *compound eyes* of other Crustacea appear to be unrepresented in the Eucopepoda, although rudiments of them were observed by Grobben in the development of *Calanus*. The *nauplius-eye*, on the other hand, is almost universally present in the free-living Eucopepoda, and even in many of the parasitic forms, and in some cases, especially among the Gymnoplea, it attains a complexity of structure not observed in any other class of Crustacea.

In the simplest and typical form it consists of three ocelli, each supplied by a separate nerve from the brain. Two of the ocelli are dorsal and look upwards and forwards, while the third is ventral, looking downwards. Each consists of a cup-shaped mass of pigment, containing in its cavity a number (up to ten) of retinal cells continuous at their distal ends with the nerve-fibres, and having (at least in some cases) a rhabdome near the proximal end. In the genus *Anomalocera* (Pontellidae) and in some Asterocheridae the number of ocelli is increased to five, those of the dorsal pair being doubled.

In some Eucopepoda the eye is movable by means of special muscles. These are wanting, however, in many cases (*Cyclops*).

In some cases the visual apparatus is perfected by the addition of a pair of corneal lenses formed by thickening of the cuticle over the dorsal pair of ocelli. These may be inconspicuous as in *Cyclops*, or large and well-defined as in *Miracia* (Harpacticidae). It is, however, in the two widely separate families of Pontellidae and Corycaeidae that the structure of the visual apparatus reaches its highest degree of complication. In the former the dorsal ocelli are often provided with cuticular lenses, and in addition there may be developed a vesicular crystalline body interposed between the retinal cells and the cuticle. The ventral ocellus approaches the sternal surface and sometimes projects as a papilliform or pedunculate prominence, while the deflected rostrum in front of it becomes thickened in such a manner as to form a biconvex lens, serving to concentrate the rays of light upon it.

In the Corycaeidae (Fig. 47) the three ocelli are widely separate and the median element remains small, while the dorso-lateral pair attain a much greater—sometimes relatively enormous—development. Each is provided with a large biconvex cuticular lens (*l*), and the retinal apparatus is at a considerable distance from this, at the apex of a conical space the base of which is formed by the lens and the walls by a delicate membrane. The pigment-cup (*p*) is elongated into a tubular form and at its mouth is set a vesicular "crystalline body" (*c*). In *Corycaeus* the posterior

part of the ocular apparatus reaches back into the region of the anterior thoracic somites, and in *Copilia* the pigment-cups enclosing the retinal cells lie together in a conical protuberance on the sternal surface of the body.

In this account it has been assumed that the "paired eyes" of Pontellidae and Corycaeidae are derived from the dorso-lateral elements of the nauplius-eye. It must be mentioned, however, that Claus, while admitting this derivation in the case of the Corycaeidae, regarded the lateral eyes of the Pontellidae as homologous with the paired compound eyes of other Crustacea. If it be the case, however, that in the Pontellid eye, as in those of other Eucopepoda, the retinal cells are "inverted" (or are connected with nerve-fibrils at the end turned towards the light), this homology would seem to be impossible.

A problematical organ to which a visual function has been attributed is found in the genus *Pleuromamma*. It lies on one side

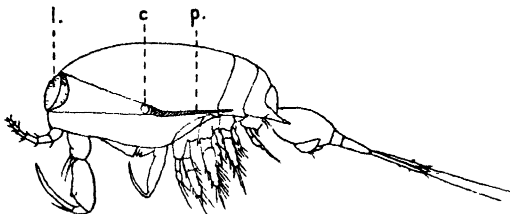


FIG. 47.

Corycaeus anglicus, male, from the side, showing one of the large paired eyes. *l*, lens; *c*, crystalline body; *p* tubular pigment-cup. (After Leuckart.)

of the cephalic shield, in the region of the maxillipeds, and consists of a globular refractive body enclosed in a mass of pigment, the whole projecting from the surface of the body in a little papilliform elevation. It has also been suggested that this is an organ of phosphorescence, but according to Giesbrecht this is not the case.

The "*aesthetascs*," or "olfactory filaments," of the antennules have already been mentioned. Their number and arrangement vary very much in different forms, and afford valuable systematic characters.

The "*frontal sense-organs*" are certain sensory setae, generally a single pair, on the front surface of the head above the rostrum, which are supplied by a pair of nerves arising from the brain, and which have been supposed to be the seat of some special sense.

The existence of "auditory" organs in the Eucopepoda is doubtful. A pair of statocysts have been described in the anterior part of the brain in *Eucalanus*.

Reproductive System.—The *ovary* may be paired or single. It is generally of small size and the ova pass at an early stage into the oviducts, which are large and give off blind diverticula (Fig. 48, *ut*). In the parasitic forms the ramifications of the oviducts (or uteri) occupy the greater part of the body-cavity, and even, in *Chondracanthus*, invade the misshapen thoracic limbs. In the terminal portion of the oviducts the walls are glandular and secrete the cement by which the eggs when expelled are agglutinated together. The openings of the oviducts are on the first abdominal somite, and may be ventral, lateral, or dorsal in position. The genital valves covering the openings have been already mentioned.

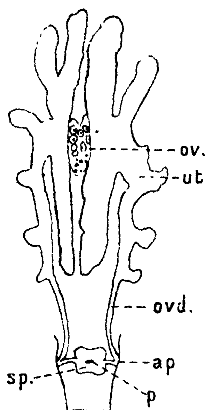


FIG. 48.

Reproductive system of female *Cyclops*. *ap*, external opening of oviduct; *ov*, ovary; *ovd*, oviduct; *p*, copulatory pore; *sp*, spermatheca; *ut*, uterine portion of oviduct. (After Hartog.)

In the great majority of Eucopepoda the female generative apparatus possesses another opening or pair of openings on the ventral side of the genital somite, serving for the entrance of the sperm and communicating internally with a single or double spermatheca (Fig. 48, *sp*). On each side the spermatheca gives off a duct which communicates with the oviduct close to its external aperture. Rarely (*Pleuromamma*) only one sperm-duct is present. This sperm-duct is lined with chitin, but, in some cases at least, the spermatheca is devoid of such a lining and is difficult to detect except when distended with spermatozoa. It is stated to be altogether absent in *Heterocope* (Gymnoplea). While the details of this apparatus have been investigated only in a relatively small number of forms, it seems probable that the possession of special copulatory pores apart from the openings of the oviducts is a characteristic of all Eucopepoda. Canu has proposed to divide the order into two groups, Monoporodelphya and Diporodelphya, according as the copulatory pore is single or paired, but it appears from Giesbrecht's researches that the two conditions may be found in closely allied forms. The last-named author has observed that in *Scottocheres* (one of the Asterocheridae) the sperm-duct opens not into the spermatheca but to the outside by a separate pore close to the opening of the latter.

The eggs are sometimes deposited singly in the water (some Gymnoplea), but in the great majority of the Eucopepoda they are cemented together into packets by means of a secretion formed by the oviduct. In all except a very few cases (Choniostomatidae) these packets are carried by the female attached to the openings of the oviducts until the eggs hatch.

The brood-pouches of the Ascidicolidae have already been alluded to.

The *testis*, like the ovary, may be paired or single, the former condition occurring chiefly among the parasitic forms. The vas deferens is sometimes developed only on one side of the body. This arrangement is universal among the Gymnoplea and is found also in some Harpacticidae. Three regions are distinguished in the vas deferens, which, however, are not sharply defined from each other. A narrow proximal portion is followed by a wider part in which the spermatozoa accumulate and become surrounded by a layer of secretion giving rise to the sheath of the spermatophore and a widened terminal part in which the development of the spermatophore is completed.

The possession of definite spermatophores seems to be a universal character of the Eucopepoda, distinguishing them from all the other "Entomostracan" orders. The spermatophores may be globular, pyriform, or, commonly, sausage-shaped, and consist of a firm cuticular (not chitinous) investment enclosing a mass of spermatozoa together with a substance which by its expansion serves to expel the spermatozoa. In addition, the spermatophore contains a coagulable secretion which is expelled before the spermatozoa and forms a sheath surrounding them within the female spermatheca. Externally the "neck" of the spermatophore is surrounded by a mass of a cementing substance secreted in the terminal portion of the vas deferens for attachment to the copulatory aperture of the female. In the Gymnoplea the last pair of thoracic feet of the male are modified to form an apparatus by which the spermatophores are transferred to the female. In the other Eucopepoda special copulatory appendages are absent.

Development of Eucopepoda.

The majority of the Eucopepoda hatch in the form of a very typical *Nauplius* larva, though many parasitic forms reach a later stage of development within the egg. The adult stage is reached by a very gradual metamorphosis, the most marked change of shape occurring (in the free-living forms) in the transition from the last metanauplius to the first "Copepodid stage." In the parasitic forms great changes occur in the later stages, some of which are described below.

The youngest nauplius stages (Fig. 6, p. 11, and Fig. 49, A) have an oval unsegmented body from which the dorsal shield is not yet defined, a large labrum, and the usual three pairs of appendages, the second pair (antennae) bearing a masticatory process, while the third pair (mandibles) are often without such a process at this stage. A large unpaired eye and a pair of antennal glands (which later degenerate) are present.

The later nauplius stages pass without any sudden change into the *metanauplius* (Fig. 49, B, C), in which the dorsal shield becomes marked off and several pairs of appendages appear as rudiments behind the mandibles. According to the earlier investigations of Claus, the second pair of these rudiments were believed to give rise to the "outer and inner maxillipeds," but, as stated above, it is now known that this is an error arising from the fact that

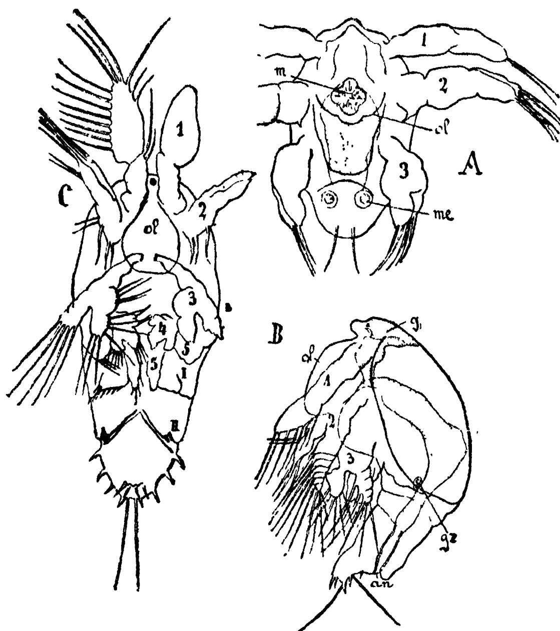


Fig. 49.

Larval stages of *Calanus finmarchicus* (= *Cetochilus septentrionalis*). A, nauplius; B, early metanauplius; C, later metanauplius. 1, antennule; 2, antenna; 3, mandible; 4, maxillula; 5, 5, maxilla and maxilliped (formerly regarded as parts of one appendage); I, II, first and second pairs of swimming-legs; *an*, anus; *g*, brain; *gz*, genital cells; *m*, mouth; *me*, primitive mesoderm cells; *ol*, labrum. (After Grobben, from Korschelt and Heider's *Embryology*.)

in the metanaupliar stages of most Copepods the appendages are very much crowded together.

The transition from the metanaupliar to the *Copepodid stages* (sometimes known as the "*Cyclops stages*") is marked by a straightening of the body, which in earlier stages is ventrally curved, and by the unsegmented posterior region becoming sharply marked off from the broader anterior part. The limbs begin to show the characters which they have in the adult, the antennules elongating and becoming divided into more numerous segments, the antennae losing the masticatory process, and the mouth-parts and swimming-feet

approximating to their permanent form. The caudal furca is also developed at this stage. There are typically four somites defined in front of the unsegmented abdominal region in the first Copepodid stage, and three pairs of swimming-feet. In each of the five succeeding Copepodid stages a somite is added, giving, together with the terminal segment or telson, the typical number of ten free segments. In the majority of cases, however, as already mentioned, the number of somites in the adult is reduced by coalescence or suppression, with corresponding changes in the course of development. The constriction which marks off the broad anterior from the narrow posterior region falls, in the first Copepodid stage, behind the third free somite. It is moved backward one somite at each moult, the Podoplea reaching the final limitation of the regions at the second and the Gymnoplea at the third Copepodid stage. In the more primitive forms (*Calanus*) the development of the limbs, like that of the somites, takes place in regular order from before backwards. In the more specialised forms, while the rudiments of the limbs appear in this order, there is a tendency for the anterior swimming-feet to outstrip in their development the maxillae and maxillipeds, which remain for some time as rudimentary buds.

Life-History of Parasitic Eucopepoda.

In no other group of Crustacea has parasitism led to such diversity of structure and of life-history as in the Eucopepoda. The parasitic habit of life has been adopted to a greater or less degree by many very different families, and every transition is found from the normal free-living types to those most completely adapted to a parasitic life.

In those Eucopepoda which, while parasitic, retain to some extent the power of locomotion, the general structure of the adult does not differ greatly from that of the free-living types and the sexual dimorphism is not accentuated. Thus in the family Asterocheridae, which have, as a rule, completely suctorial mouth-parts and are parasitic on various Invertebrata, most of the species are capable of swimming and retain the general Copepod form. In the Ascidicolidae, which live rather as commensals than as parasites in the alimentary tract of Tunicata and Echinoderma, we find a series leading from the little-modified forms (*Notodelphys*, etc.) which live in comparative freedom in the pharyngeal sac of the Tunicata, and in which the adults of both sexes possess natatory thoracic limbs, to those species which live in the stomach and intestine, and have assumed in the female an almost vermiform shape, with limbs adapted to push their way through the contents of the alimentary canal of the host. The male in most cases is free-swimming, at least in the adult stage, and is correspondingly less modified in general form.

As an example, we may take *Enterognathus*, recently described by Giesbrecht. This form differs from most other Ascidicolidae in infesting, not a Tunicate, but the Crinoid *Antedon rosacea*. The female (Fig. 50) has an elongated body which presents the full number of segments. Antennules and antennae are short and consist of few segments. The mouth-parts are not suctorial. The mandible consists of a long and narrow blade, with toothed cutting edge and a vestigial palp of two segments. The maxillipeds are absent. The first four pairs of thoracic feet are short and biramous, with the endopodite forming a broad, spoon-like plate, without setae, while the exopodite forms a strong curved claw. By movements of these feet, and by elongation and contraction of the body, the parasite pushes its way through the contents of the intestine of its host. The last pair of feet are broad lamellae fringed with hairs, covering the point of attachment of the egg-masses, and preventing these from being detached in the movements of the animal. The abdomen ends in a well-marked furca, bearing a few short setae.

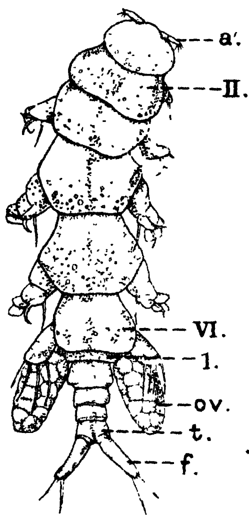


Fig. 50.

Enterognathus comatulae, adult female, × 17. (After Giesbrecht.) II, VI, second and sixth thoracic somites; 1, first abdominal somite; *a'*, antennule; *ov*, egg-mass; *t*, telson; *f*, caudal furca.

The *male* is free-swimming, and presents the typical Copepod form, with fully segmented body and natatory thoracic feet. Its most striking feature is the entire absence of mouth-parts, there being no trace of the appendages between the antennae and the first pair of swimming-feet.

The life-history is as follows. The earlier stages are unknown, but it appears that the first Copepodid stage is free-swimming, and that both sexes enter the alimentary canal of the host in the second Copepodid stage. Retrogressive changes then take place, the succeeding stages of the female resembling the adult in general shape, while those of the male lose the natatory setae of the thoracic feet. In the adult male, however, these are reacquired, while the mouth-parts disappear and the animal escapes from the host. Where it meets with the female is not definitely known, but it is at least probable that the latter temporarily leaves the alimentary canal of the Crinoid, and clinging to the surface of its body, is there fertilised by the male.

In certain families of the truly parasitic forms with suctorial mouth-parts (Caligidae, Lernaeidae, Lernaeopodidae) a community

of origin is indicated by the possession of a larval glandular organ of adhesion in the frontal region (Fig. 45, A, *f.gl*). In the Caligidae the first Copepodid stage becomes attached to the skin of a fish by a long filament (frontal band) which appears to be formed by the consolidated secretion of a convoluted tubular gland lying in the frontal region. Larvae in this stage were described by Burmeister as a distinct genus, under the name *Chalimus*, and it may conveniently be designated the *Chalimus*-stage. In later stages both sexes become free, and in some species at least retain the power of swimming freely, attaching themselves only temporarily to fishes for the purpose of sucking their blood. The males and females, at the stage at which fertilisation takes place, do not differ greatly, but after impregnation the genital somite of the female becomes greatly distended and filiform egg-masses are produced.

A more complex life-history is that of the Lernaeidae. *Lernaea branchialis* is hatched as a nauplius, and when it reaches a stage corresponding to the first Copepodid stage (Fig. 51, A) it becomes parasitic on the gill-filaments of a fish, usually one of the Pleuronectidae, attaching itself at first by the subchelate antennae and the maxillae, and later by the frontal cement-gland. It then passes into a "pupal" stage (Fig. 51, B), in which the power of movement is lost and retrogressive changes occur, especially in the swimming-legs, which lose their setae and become unsegmented stumps. Later, the power of locomotion is regained, and the parasite leaves its first host in a form which corresponds to the adult stage of free-living Copepods. Sexual maturity is now reached and the female (Fig. 52, B) is distinguished by the great elongation of the region of the genital segment. Impregnation takes place in this free-swimming stage and the male does not develop further. The female, however, seeks a second host, a fish of the family Gadidae, and becoming attached to the gills, burrows into the flesh so that the whole anterior region of the

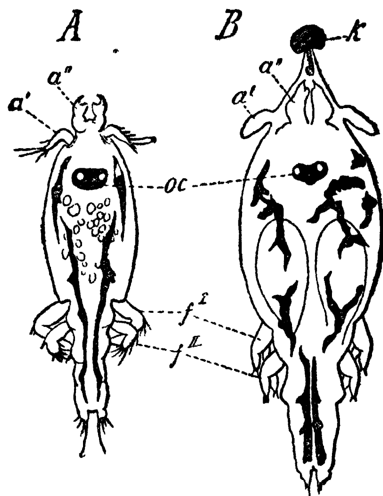


FIG. 51.

Two larval stages of *Lernaea branchialis*. A, first Copepodid stage. B, pupal stage. *a′*, antennule; *a″*, antenna; *f′*, *f″*, first and second pairs of swimming-feet; *k*, mass of cement produced by frontal gland; *oc*, nauplius-eye. (After Claus, from Korschelt and Heider's *Embryology*.)

body is embedded. Three ramified processes grow out from the head into the tissues of the host, and the region of the genital somite becomes enormously enlarged, forming the greater part of

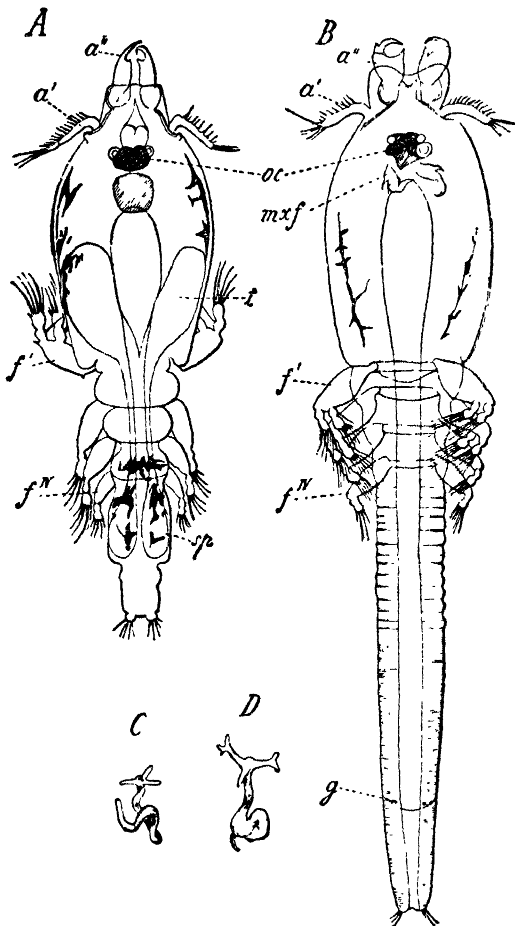


FIG. 52.

Lernaea branchialis. A, male; B, female, at copulatory stage. C, D, later stages of female after attachment to second host. *a'*, antennule; *a''*, antenna; f^{i}, f^{iv}, first and fourth pairs of swimming-feet; *g*, opening of spermatheca; *mxf*, maxilliped; *oc*, nauplius-eye; *sp*, spermatophore sac; *t*, testis. (After Claus, from Korschelt and Heider's *Embryology*.)

the vermiform body (Fig. 52, C, D). The swimming-feet are retained in a vestigial condition near the anterior end.

In some other forms parasitic on fish (Lernaeopodidae, Chondracanthidae) the male is attached to the female in a dwarfed condition throughout life. The larva becomes parasitic in the

first Copepodid stage, and the later stages of the typical series are suppressed, the characteristic features of the parasite being assumed at the next moult.

In the Choniostomatidae, which are parasitic on other Crustacea, the larva hatches in the first Copepodid stage, with two pairs of swimming-feet, and becomes attached to the host by an adhesive frontal plate, corresponding probably to the "frontal thread" of other forms. This larva may give rise at once to the adult form, or a pupal stage with reduced limbs may intervene. The male is similar to the female in essential structure, but of much smaller size.

The most extreme stage of degeneration is reached in the Herpyllobiidae, which are parasitic on Polychaete worms and on Crustacea. In *Rhizorhina*, which is the most thoroughly known, the adult female is entirely without appendages, and is attached by a tubular process which ramifies within the body of the host in a fashion recalling the "roots" of the Rhizocephala. The adult male is also entirely limbless, but remains enclosed within the last larval skin (of the first Copepodid stage). Within it are formed a pair of relatively enormous spermatophores, which are not expelled from the body but discharge their contents through ducts which pass out close to the point of attachment, and *in front of* the position of the larval mouth. A number of males are attached to the body of the female near the genital apertures.

The Monstrillidae have a very remarkable life-history, which has only recently been made known. The adults of both sexes are free-swimming, and are without mouth-parts or alimentary canal. The newly hatched young are also free-swimming, but the intermediate stages are endoparasitic within various Polychaete annelids. The life-history is most fully known in the case of *Haemocera danae*, investigated by Malaquin (Fig. 53). The adults (F) have antennules and four pairs of swimming-feet, but no trace of antennae or mouth-parts. The fifth pair of thoracic feet are vestigial in the female and are stated to be absent in the male. The alimentary system is represented by a blind stomodaeal invagination and a mass of undifferentiated endoderm cells. The female carries a single packet of eggs (*ov*) adhering to a pair of very long setae (*g.s*) which spring from the genital valves. The young are hatched as nauplii, without mouth or alimentary canal, and with strong hook-like mandibles (A). The nauplius burrows into the body of its host (the Polychaete *Salmacina*), casting its cuticle in the process and losing its limbs, so that when it reaches the body-cavity it consists merely of a mass of embryonic cells without a cuticle (B). From the body-cavity the parasite passes into the vascular system of the host, where it undergoes its further development. A thin cuticle is now secreted, and a pair of processes begin to grow out from one end of the ovoid body (C, *pr*). These

increase in size, in some cases, to several times the length of the body, and as the cuticle covering them is very thin it is believed

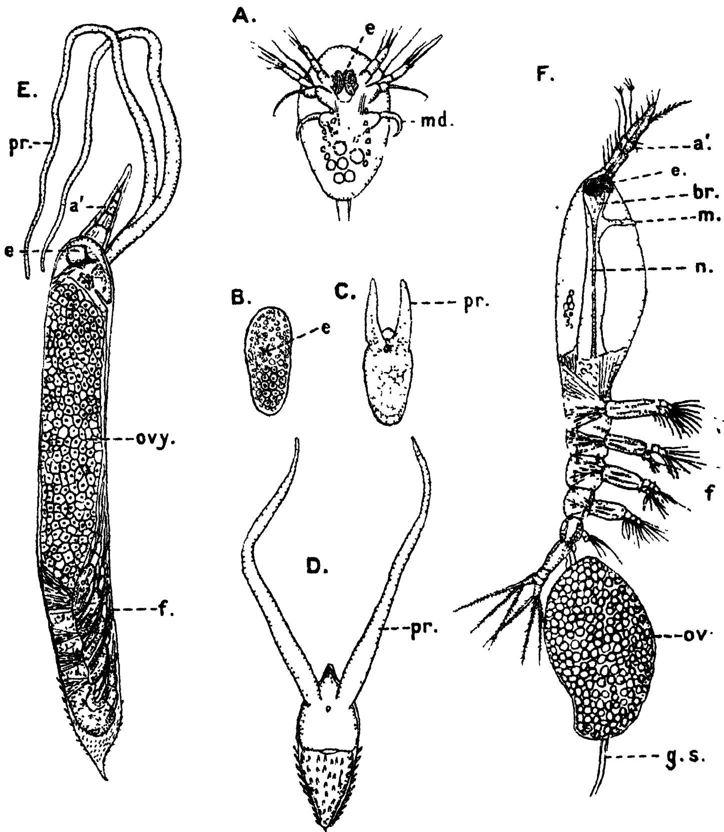


FIG. 53.

Stages in the life-history of *Haemocera danae*. A, free-swimming nauplius-larva, × 280. B, embryo after penetrating into the body-cavity of the host; no organs remain except the degenerating nauplius-eye. C, later stage, from the vascular system of the host; the absorptive processes have begun to develop. D, still later stage; the absorptive processes are fully formed and the posterior end of the embryo is provided with rows of recurved hooks. E, the adult female, just before emergence from the host; the anterior part of the body is distended with eggs. F, free-swimming female, carrying the extruded eggs, × 28; the hypodermis in the anterior part of the body has separated from the cuticle after expulsion of the eggs and forms a sheath around the nerve-cord. *a'*, antennule; *br*, brain; *e*, nauplius-eye; *f*, swimming-feet; *g.s*, genital setae; *m*, position of mouth; *md*, mandible of nauplius; *n*, nerve-cord connecting brain with ventral nerve-chain; *ov*, mass of eggs carried on genital setae; *ovy*, ovary; *pr*, absorptive processes. (After Malaquin.)

that they act as absorptive organs. In some cases, but not always, a second pair of these processes is found behind the first. From the position which they occupy relatively to the rudiments of

appendages afterwards appearing, it is believed that they represent the antennae and mandibles of the nauplius. The organs of the adult are gradually differentiated within the cuticular sac, which enlarges with the growth of the animal. The pointed posterior end of the sac is surrounded by rows of recurved hooks (D), and these appear to be used in boring a way out through the tissues of the host when development is complete (E). The reproductive organs are developed before the parasites escape from the host. After escaping, a single moult takes place and sexual maturity is reached.

The life-history of the Monstrillidae may be compared with that of the male *Enterognathus* described above, in which the earlier larval stages and the adult are free-swimming, while the intervening stages are parasitic and degenerate, and in which also the adult is incapable of feeding.

Morphology of Branchiura.

The body is much flattened, and is divided into three regions, an unsegmented, cephalothoracic region followed by three free thoracic somites and an unsegmented abdomen (Fig. 54). The cephalothoracic region is covered by a greatly developed head-shield or carapace, which, while not projecting beyond the articulation of the succeeding somite as a distinct "shell-fold," is expanded on each side in a great wing-like pleural fold. In many species the lateral folds are produced backwards and cover the thoracic somites and their appendages, and sometimes even the abdomen. The abdomen is notched or bilobed, and bears a pair of minute furcal rami (*f*).

Appendages.—The *antennules* are small, consisting of four segments, of which the first is divided into two parts and is provided with a large hooked claw and some smaller spines, used for attachment to the host. The *antennae* are also short, uniramous in the adult, of four segments, the basal part provided with stout spines.

The mouth-parts are suctorial, the upper and lower lips together forming a proboscis (Fig. 54, *p*) within which are enclosed the mandibles and maxillulae. The maxillulae are never included in the proboscis in suctorial Eucopepoda.

The *mandibles* are without palps in the adult and have sickle-shaped, serrated tips. The *maxillulae* are stated to be wanting in the genus *Dolops*. In *Argulus* they are simple, lancet-like blades. The *maxillae* ("first maxillipeds") are very remarkably modified. Except in the genus *Dolops*, where they end in stout hooked claws, they are represented chiefly by a pair of large adhesive suckers (Fig. 54, *mx″*), situated some distance in front of the proboscis. The sucker is developed from the basal portion of the appendage, the

distal segments which are present in the larva persisting as a vestige under the outer margin of the sucker or disappearing altogether. The sucker itself is provided with strong muscles and its margin is strengthened by radiating chitinous rods.

The *first thoracic appendage* ("second maxilliped") (*mxp*) consists of five segments, the basal one produced into a lobe armed with strong teeth and the end of the limb carrying two stout claws.

The next four pairs of appendages are biramous natatory feet. The first pair is attached to the cephalothoracic region, the remaining three correspond to the three free thoracic somites. Each consists of a stout protopodite, which, in some species at least, has

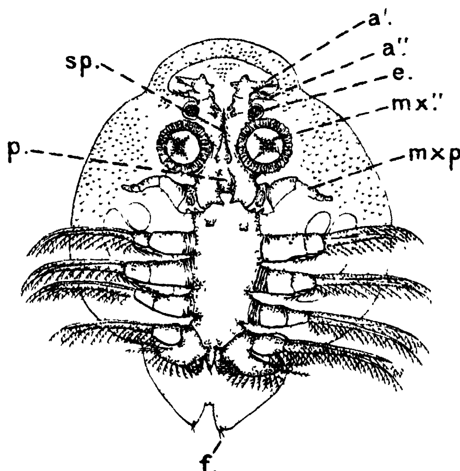


Fig. 54.

Argulus americanus, female, from below, × 5. *a'*, antennule; *a''*, antenna; *e*, paired eye; *f*, caudal furca; *mx''*, sucker formed by maxilla ("first maxilliped"); *mxp*, first thoracic appendage ("second maxilliped"); *p*, suctorial proboscis; *sp*, poison spine. (After Wilson.)

three segments, and an exopodite and endopodite of about equal length. The exopodite is unsegmented, and the endopodite consists in the first pair of three segments, in the second of one, and in the last two pairs of two segments. Both rami are furnished with two rows of long plumose setae, set along the dorsal and ventral margins respectively. The insertion of the broadened bases of these setae gives to the exopodite and endopodite the appearance of being divided into numerous short segments, and they have been so described, but the arrangement of the musculature shows that these do not represent true segments of the limb.

On certain of the anterior legs in most of the species the protopodite carries at its distal end, besides the endopodite and exopodite, a slender appendage, known as the *flagellum*, which

originates to the outer (or dorsal) side of the exopodite, and is bent backwards upon the protopodite. It is provided with two rows of plumose setae, and its probable function is to cleanse the lower surface of the carapace. The homology of this appendage is doubtful. It cannot be an epipodite since it springs from the distal segment of the protopodite. Nothing equivalent to it is found in the Eucopepoda.

In the male sex the peduncles of the last two, sometimes of the last three, pairs of legs are modified for purposes of copulation. The details differ in the different species, but in all the peduncle of the penultimate pair is excavated to form a seminal pouch which

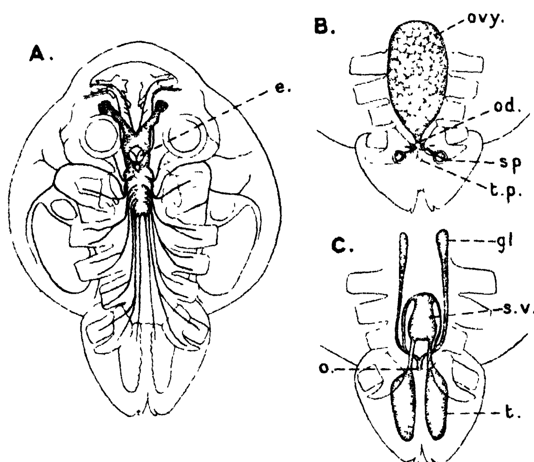


Fig. 55.

A, nervous system of *Argulus americanus*. *e*, nauplius-eye; immediately below is the opening through which the oesophagus passes. B, female reproductive organs. *ovy*, ovary; *od*, opening of oviduct; *sp*, spermatheca; the papillae on which the spermatheeal ducts open are seen just below the opening of oviduct; *t.p*, "tactile papillae." C, male reproductive organs. *gl*, accessory gland; *o*, external opening; *s.v*, seminal vesicle; *t*, testis. (After Wilson.)

opens on the dorsal surface of the limb. On the anterior surface of the peduncle of the last pair is a peg-like process which seems to be used for opening the mouth of the seminal pouch so that the latter can be filled with sperm. In some species in the female sex a pair of finger-like processes (Fig. 55, B, *t.p*) are situated at the sides of the genital orifice between the last pair of legs. These may possibly represent a vestigial sixth pair of thoracic appendages.

In the genus *Argulus* a very peculiar poison apparatus is situated in front of the mouth. It consists of a hollow spine (Fig. 54, *sp*), which can be withdrawn into and protruded from a sheath by the action of special muscles. The duct which traverses it communicates with three groups of large unicellular glands lying at its

base. These glands appear to be a specialisation of some of the dermal glands which (as in many Eucopepoda) are abundantly distributed over the surface of the body.

Alimentary System.—The alimentary canal has a narrow oesophageal region, with strong circular and longitudinal muscles, which projects, funnel-like, into the wide stomach. The latter gives off a pair of diverticula, which are much ramified, and occupy the greater part of the lateral lobes of the cephalothorax. When feeding, these diverticula, as well as the stomach and intestine, become filled with the juices of the host. The stomach is followed by a wide intestinal region which is separated by a sphincter from the narrow rectum. The latter is without the dilator muscles found not only in Eucopepoda but in most Crustacea.

Circulatory System.—The heart is situated at the junction of thorax and abdomen, and sends off an aorta which reaches as far forward as the brain. It is provided with one or two pairs of lateral and inferior afferent ostia and sometimes a median inferior efferent opening at the base of the aorta. There appears to be doubt as to the existence of a posterior median efferent opening. In the earliest larval stages the heart is absent, and the circulation is mainly carried on, as in the later stages it is assisted, by rhythmical contractions of dorso-ventral muscles in the abdomen.

Excretory System.—An excretory gland of the usual type is present, and has been identified as the maxillary gland (shell-gland). It appears from the investigations of Claus and of Nettovich, however, that it differs from the maxillary gland of the Eucopepoda and other Crustacea in opening not on the maxilla but on the first thoracic limb (the so-called "second maxilliped"), or on the sternal surface of the body close to the base of that appendage.

Nervous System.—The ventral nerve-chain (Fig. 55, A) is shortened, but six ganglia can be distinguished. The statements as to the origin of the nerves to the two pairs of maxillipeds are conflicting, but the last four ganglia supply the somites of the four pairs of swimming-feet, the last also sending nerves to the abdomen.

Sense-Organs.—A median (nauplius) eye of the usual structure is set upon the dorsal surface of the brain (Fig. 55, A, *e*). In addition, there are a pair of large compound eyes (Fig. 54, *e*) visible through the transparent integument of the dorsal surface. Each is supplied by a stout optic nerve which swells into a ganglion before entering the eye. The eye is movable, but it differs from the similarly movable, non-pedunculated eyes of the Branchiopoda in the fact that it moves not in a "corneal pouch" but in a blood-space which intervenes between the outer ends of the quadripartite crystalline bodies and the integument. Seen from above this blood-sinus is bounded on the anterior, external,

and posterior sides by a chitinous wall. It seems not unlikely that further research will show the wall to be formed by an invagination of the cuticle, in which case it may represent the vestige of a corneal pouch like that of the Branchiopoda.

Reproductive System.—The ovary (Fig. 55, B, *ovy*) is unpaired and, at its first appearance in the larva, asymmetrically placed, afterwards assuming a median position. Rudiments of two oviducts are found in the larva, but that situated on the same side of the body as the ovary atrophies, while the other develops further and ultimately opens (*od*) in the middle line between the bases of the last pair of legs.

A pair of spermathecae (Fig. 55, B, *sp*) are found in the abdomen. They are not connected with the oviducal opening, but each has a short duct which gives off a blind diverticulum and terminates on a papilla with a retractile spiniform tip close to the anterior margin of the abdomen. It is believed that the sharp points of these papillae pierce the envelopes of the eggs when the latter are laid, so as to permit the entrance of the spermatozoa. The eggs are laid attached to stones or other objects.

The testes (Fig. 55, C, *t*) are paired and lie in the abdomen. Their ducts unite to form an unpaired seminal vesicle (*s.v*), and after receiving the ducts of a pair of accessory glands (*gl*) lying in the thoracic region again unite to open by a median pore (*o*) between the bases of the last pair of legs. The seminal pouches on the penultimate legs of the male and the structures connected therewith have already been mentioned.

Development of Branchiura.

In some species of *Argulus* the newly hatched larva has all the appendages similar to those of the adult with the exception of the first maxillipeds, which are not modified into suckers but are stout clasping limbs, each consisting of four segments and ending in a double claw. In other species, however, among which is the common European *A. foliaceus*, the newly hatched larva differs still more from the adult (Fig. 56). The antennae are biramous, having a large unsegmented exopodite which is lost in the adult, and the mandibles have a large uniramous palp of two segments. The antennal exopodite and the mandibular palp are tipped with plumose setae and serve as swimming-organs. The heart is not found in the earliest larvae but develops after the first moult.

Remarks on Habits, etc.

The majority of the Eucopepoda are marine, but numerous species, belonging chiefly to the families Centropagidae, Harpac-

ticidae, and Cyclopidae, are very abundant in fresh water. Most of the Gymnoplea are pelagic, forming a very important part of the plankton of the sea and of lakes. The non-parasitic Podoplea, on the other hand, with the exception of a few pelagic groups like the Corycaeidae, belong to the bottom-fauna. A large

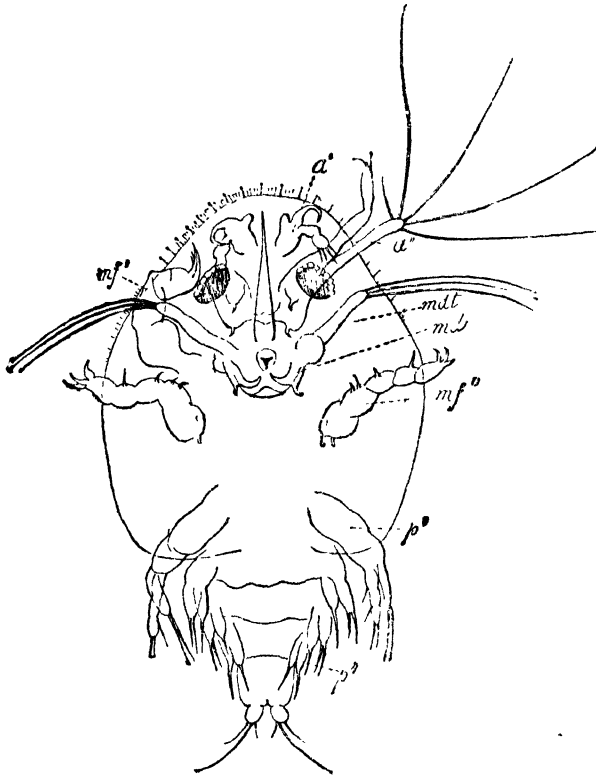


FIG. 56.

Newly hatched larva of *Argulus foliaceus*. *a'*, antennule; *a''*, antenna; *md*, mandible, *mdt*, mandibular palp; *mf'*, maxilla (first maxilliped); *mf''*, (second) maxilliped; p^1, p^4, first and fourth pairs of swimming-feet. (After Claus, from Korschelt and Heider's *Embryology*.)

proportion of the parasitic forms of various families attack fish, and some of these, such as *Lernaeocera* and *Achtheres*, occur in fresh water. *Pennella* is sometimes found on whales. Other parasitic and semi-parasitic forms are found on various groups of marine invertebrates. The Branchiura are temporary parasites on fish and occur both in the sea and in fresh water.

Most of the free-living Eucopepoda are minute, but some of the

parasitic species attain a greater size, the largest (*Pennella*) being more than a foot in length.

No fossil remains of Copepoda are known.

Affinities and Classification.

On the hypothesis that the Nauplius represents the ancestral type of the Crustacea, the Eucopepoda would be regarded as the most primitive existing members of the class, retaining, as they do, naupliar characters in the form of the first three pairs of appendages and in the absence of paired eyes and of a shell-fold. As already indicated, however, it is much more probable that they are to be regarded as a specialised and in some respects degenerate group which, while retaining, in some cases, a very primitive structure of the cephalic appendages, has diverged from the ancestral stock in the reduction of the number of somites, the loss of the paired eyes and shell-fold, and the simplified form of the trunk-limbs. The prevalence of parasitism and the great structural changes associated therewith render the classification of the Eucopepoda a matter of peculiar difficulty, and none of the schemes hitherto proposed is altogether satisfactory. In Claus's system (1880) the distinction drawn by most of the older authors between free-living and parasitic forms is still maintained in the two chief divisions of Gnathostomata and Siphonostomata, the latter including forms in which the mouth-parts are more or less distinctly suctorial. Giesbrecht has shown, however, that this arrangement, and also that proposed by Canu, based on the copulatory pores of the female, are quite unnatural, since forms with biting and suctorial mouth-parts and with paired and unpaired copulatory pores may occur within the limits of the same family. Giesbrecht's own classification of the Eucopepoda, which is given below, marks a distinct advance, especially as regards the separation of the more primitive pelagic families to form the group Gymnoplea. His arrangement of the remaining families, which he groups together as Podoplea, is, however, less convincing, and he does not attempt to define the position of many of the parasitic forms. The system is therefore incomplete and can only be adopted as a temporary expedient pending further investigation.

Some modern writers follow Zenker and Thorell in referring the Branchiura to the Branchiopoda, although the only character which can now be referred to in support of this arrangement is the presence of paired compound eyes. On the other hand, the comparison instituted by Claus between the appendages of Branchiura and Eucopepoda shows a general similarity of structure which cannot be disregarded. The only serious difficulty in the way of this comparison is the difference in the position of the maxillary gland,

which in the Eucopepoda, as in other Crustacea, opens on the maxilla, but in the Branchiura on the first thoracic appendage. It seems more probable, however, that a shifting of the aperture has taken place than that the appendages do not correspond serially in the two groups.

SUB-CLASS COPEPODA, H. Milne-Edwards (1830).

ORDER 1. **Eucopepoda**, Claus (1875).

Paired compound eyes absent; genital apertures on the seventh trunk-somite; thoracic limbs without flagellum; fertilisation by spermatophores.

SUB-ORDER 1. **Gymnoplea**, Giesbrecht.

Last thoracic somite firmly connected with the preceding somite and movably articulated with the first abdominal somite; last pair of thoracic appendages in female similar to preceding pair, or reduced or absent, in male always present and modified as copulatory organs; one or neither of the antennules geniculate in male; eggs deposited singly or carried in a single packet; heart generally present; vas deferens unpaired, its opening unsymmetrically placed. Free-living forms, mostly pelagic.

TRIBE 1. AMPHASKANDRIA, Giesbrecht.

Antennules of male not geniculate, with more numerous aesthetascs than in female.

Family CALANIDAE. This extensive group is divided by Sars into twelve families. Most of these correspond to sub-families recognised by Giesbrecht. *Calanus*, Leach (Fig. 41); *Eucalanus*, Dana; *Rhincalanus*, Dana; *Calocalanus*, Giesbrecht (Fig. 42); *Paracalanus*, Boeck; *Pseudocalanus*, Boeck; *Aetideus*, Brady; *Euchaeta*, Philippi; *Phaenna*, Claus; *Scolecithrix*, Brady; *Diaixis*, G. O. Sars; *Stephos*, Scott; *Tharybis*, G. O. Sars; *Pseudocyclopia*, Scott. (The families represented by the last eight genera are separated from the Amphaskandria by Sars to form a division Isokerandria.)

TRIBE 2. HETERARTHRANDRIA, Giesbrecht.

One of the antennules geniculate in male.

Family CENTROPAGIDAE. Divided into eight families by Sars:—*Centropages*, Kroyer; *Diaptomus*, Westwood; *Pseudodiaptomus*, Herrick; *Heterocope*, G. O. Sars; *Lucicutia*, Giesbrecht; *Temora*, Baird; *Metridia*, Boeck; *Heterorhabdus*, Giesbrecht; *Pleuromamma*, Giesbrecht; *Arietellus*, Giesbrecht. Family PSEUDOCYCLOPIDAE. *Pseudocyclops*, Brady. Family CANDACIIDAE. *Candacia*, Dana. Family PONTELLIDAE. Divided into four families by Sars:—*Pontella*, Dana; *Parapontella*, Brady; *Acartia*, Dana; *Anomalocera*, Templeton; *Tortanus*, Giesbrecht.

SUB-ORDER 2. **Podoplea,** Giesbrecht.

(Most of the following characters are subject to modification in parasitic forms.)

Last thoracic somite movably articulated with the preceding, and firmly united with the first abdominal somite, which it resembles in size and form. Last pair of thoracic feet vestigial in both sexes; not modified as copulatory organs in male. Both or neither of the antennules geniculate in the male. Eggs generally carried in paired or unpaired masses. Heart absent (except in *Misophria*). Male reproductive system usually paired. Free-living (rarely pelagic) or parasitic.

TRIBE 1. ISOKERANDRIA, Giesbrecht.

Swimming forms with antennules not geniculate in male, generally similarly segmented in both sexes, and parasitic forms allied to these.

Family CLAUSIDIIDAE. *Clausidium*, Kossmann. Family CORYCAEIDAE. *Corycaeus*, Dana (Fig. 47); *Copilia*, Dana; *Sapphirina*, J. V. Thompson. Family ONCAEIDAE. *Oncaea*, Philippi. Family LICHOMOLGIDAE. *Lichomolgus*, Thorell. Family ERGASILIDAE. *Ergasilus*, Nordmann. Family BOMOLOCHIDAE. *Bomolochus*, Nordmann. Family CLAUSIIDAE. *Clausia*, Claparède. Family NEREICOLIDAE. *Nereicola*, Keferstein.

TRIBE 2. AMPHARTHRANDRIA, Giesbrecht.

Swimming forms, with both antennules geniculate in male, generally differently segmented in the two sexes, and parasitic forms allied to these.

Family MISOPHRIIDAE. *Misophria*, Boeck. Family HARPACTICIDAE. This extensive group corresponds rather to an assemblage of families (cf. Sars):—*Harpacticus*, Milne-Edwards; *Longipedia*, Claus; *Cerrinia*, Norman; *Ectinosoma*, Boeck; *Peltidium*, Philippi; *Tegastes*, Norman; *Porcellidium*, Claus; *Idya*, Philippi; *Thalestris*, Claus; *Diosaccus*, Boeck; *Canthocamptus*, Westwood; *Belisarius*, Maupas; *Laophonte*, Philippi; *Setella*, Dana; *Miracia*, Dana; *Aegisthus*, Giesbrecht; *Clytemnestra*, Dana. Family CYCLOPIDAE. *Cyclops*, Muller; *Oithona*, Baird. Family MONSTRILLIDAE. *Monstrilla*, Dana; *Haemocera*, Malaquin (Fig. 53). Family ASCIDICOLIDAE. *Ascidicola*, Thorell; *Notodelphys*, Allman, *Doropygus*, Thorell; *Notopterophorus*, Costa; *Enterognathus*, Giesbrecht (Fig. 50). Family ASTEROCHERIDAE. *Asterocheres*, Boeck; *Acontiophorus*, Brady (Fig. 44); *Cancerilla*, Dalyell; *Scottocheres*, Giesbrecht; *Artrotrogus*, Boeck (Fig. 46). Family NICOTHOIDAE. *Nicothoe*, Audouin. Family DICHELESTIIDAE. *Dichelestium*, Hermann; *Lernanthropus*, Nordmann.

The position of the remaining families (consisting wholly of parasitic forms) with respect to this system of classification is not yet determined. The groups most usually accepted are:—

Family CALIGIDAE. *Caligus*, Muller. Family LERNAEIDAE. *Lernaea*, Linn. (Figs. 51, 52); *Pennella*, Oken; *Lernaeocera*, Blainville. Family LERNAEOPODIDAE. *Lernaeopoda*, Kroyer; *Achtheres*, Nordmann (Fig. 45). Family CHONDRACANTHIDAE. *Chondracanthus*, La Roche. Family

Choniostomatidae. *Choniostoma*, Hansen. Family Herpyllobiidae. *Herpyllobius*, Steenstrup and Lütken; *Rhizorhina*, Hansen.

Order 2. **Branchiura**, Thorell (1864).

Paired compound eyes present; genital apertures on fifth trunk-somite; thoracic limbs sometimes with flagellum; no spermatophores.

Family Argulidae. *Argulus*, O. F. Muller (Fig. 54); *Dolops*, Audouin; *Chonopeltis*, Thiele.

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CHAPTER V

THE CIRRIPEDIA

SUB-CLASS CIRRIPEDIA, Burmeister (1834).

Order 1. **Thoracica.**
  Sub-Order 1. **Pedunculata.**
  ,, 2. **Operculata.**
    Tribe 1. Asymmetrica.
    ,, 2. Symmetrica.
,, 2. **Acrothoracica.**
,, 3. **Ascothoracica.**
,, 4. **Apoda.**
,, 5. **Rhizocephala.**

Definition.—Crustacea which are sessile in the adult condition; the carapace (very rarely absent) forms a mantle completely enclosing the body and limbs, usually strengthened by shelly plates; the posterior limbless part of the trunk is vestigial and usually ends in a caudal furca; the antennules are organs of attachment, becoming vestigial in the adult, and the antennae generally disappear; mandibles without palp; typically six pairs of biramous cirriform trunk-limbs; usually hermaphrodite, female genital apertures on first trunk-somite, male apertures behind last pair of limbs; paired eyes absent in adult; development with metamorphosis; young generally hatched in nauplius stage and passing through a so-called "cypris stage" with bivalved shell.

Historical.—Some of the Cirripedia are sufficiently common and conspicuous to have attracted attention from remote times. They are probably referred to by Aristotle, and they formed the subject of a curiously persistent mediaeval myth, current in literature from the twelfth to the beginning of the eighteenth century, regarding the origin of the Barnacle Goose. While the earlier systematists not unnaturally classed the barnacles and acorn-shells as Mollusca, it seems strange to find this view of their affinities surviving the

anatomical investigations of Cuvier. Lamarck, who was the first to give them the name "Cirrhipèdes" (later corrected by Burmeister to Cirripedia), referred more or less vaguely to their affinities with Crustacea, as did also Oken and others, without definitely removing them from the Mollusca.

It was not until J. Vaughan Thompson, in 1830, described the development of *Balanus* from the "*Cypris*" larva that the Crustacean nature of the group was placed beyond dispute. A little later Burmeister (1834) and Thompson himself (1835) completed the outline of the life-history by discovering the earlier nauplius stage, confirming the long-forgotten observations of Slabber, who had figured the nauplius of *Lepas* as early as 1767. Although notable contributions to the anatomy of the group were made by Martin Saint-Ange (1835) and others, its taxonomy remained in the hands of conchologists, and new genera and species were established on the superficial characters of the shell alone. It is curious to note, as a survival of this period, that so recently as 1906 it was thought necessary to include a chapter on Cirripedes in a conchological work. Darwin's *Monograph of the Cirripedia* (1851-54) placed the study of the group upon a new basis, and indeed still remains the chief work of reference on the subject. The discovery of the "complemental males" and of the remarkable genera *Cryptophialus* and *Proteolepas* (the latter not since re-observed) are due to Darwin, while his systematic treatment of the normal Cirripedia (Thoracica) has scarcely been modified by subsequent workers, except as regards the addition of new species, for the most part from the deep sea. Some anatomical errors in Darwin's work were soon after corrected by Krohn (1859). J. V. Thompson had already in 1836 pointed out the resemblance of the nauplius larva of *Sacculina* to that of the Cirripedia, and Lilljeborg (1859-60) established for that genus and its allies the group of "Cirripedia Suctoria," and showed that they passed through a "*Cypris*" stage. Fritz Müller (1862-63) gave a more detailed account of the anatomy and larval stages of this group, to which he gave the name Rhizocephala. Delage, in a remarkable memoir (1884), made known, for the first time, the complete life-history of *Sacculina*, and his results, though received with scepticism by some, have recently been confirmed by G. Smith (1906). The group of Ascothoracica was established by Lacaze-Duthiers (1883) for the very remarkable genus *Laura*, and other genera have been added by Norman, Fowler (1889), Knipowitsch, and others. Among the more important contributions to the study of the normal Cirripedes may be mentioned the works of Hoek on the "Challenger" collections (1883-84), Aurivillius (1892-95), and Gruvel (1904), and on the larval stages those of Claus (1869), Groom (1895), and Hansen (1899)

MORPHOLOGY OF THORACICA AND ACROTHORACICA.

In general form and in many details of structure the Cirripedia as a whole depart more widely from the common type than do any of the other sub-classes of the Crustacea. This is correlated with the sessile habit of life which is universal within the group. In those forms which have become purely parasitic, as in the orders Ascothoracica, Apoda, and Rhizocephala, the modifications are still more profound, leading, in the last-named order, to the disappearance of every trace of Arthropod organisation. Nevertheless, the life-history and even the minute characters of the larvae are so constant throughout the group that it is impossible to question the close relationship of the various forms.

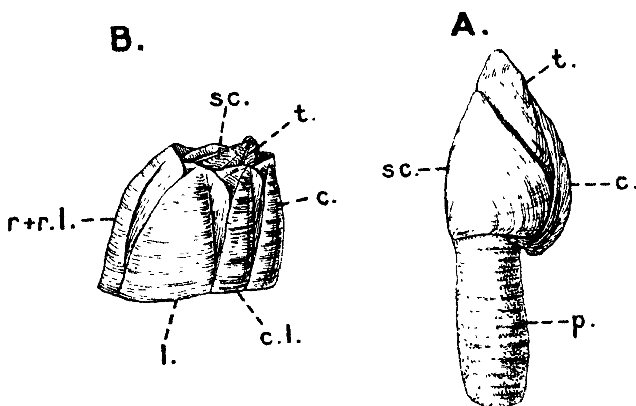


FIG. 57.

A. *Lepas anatifera*; B. *Balanus hameri*. (After Darwin.) *c*, carina; *c.l*, carino-lateral; *l*, lateral; *p*, peduncle; *r+r.l*, rostrum coalesced with rostro-lateral; *sc*, scutum; *t*, tergum.

Leaving aside for the present the parasitic orders named above, the remaining Cirripedia, forming the orders Thoracica and Acrothoracica (Abdominalia of Darwin), show considerable uniformity of structure, though differing widely in general appearance. In all cases, the animal is attached to some foreign object by the anterior portion of the body in the region of the antennules. The shell-fold is greatly developed, forming a "mantle" enclosing the body and limbs, and strengthened, as a rule, by shelly plates on its outer surface. Owing to a strongly marked dorsal flexure of the preoral region, the greater part of the body within the mantle comes to lie nearly at right angles to the anterior part. The anterior part of the cephalic region may be elongated into a flexible and muscular *peduncle* (Fig. 57, *p*), as in the Pedunculata, or represented only by

a flattened disc of attachment, as in the Operculata and Acrothoracica. When a peduncle is present, the rest of the body enclosed by the mantle is distinguished as the *capitulum*.

On account of the confusion which would arise from applying the usual terms of orientation to animals of such complex form, it is customary, in describing Cirripedia, to employ an arbitrary terminology in which the animal is supposed to be placed vertically with the capitulum above, and the peduncle or base of attachment below. What is, morphologically, the sternal aspect of the peduncle and the anterior side of the capitulum is called the "rostral," the opposite being the "carinal" side.

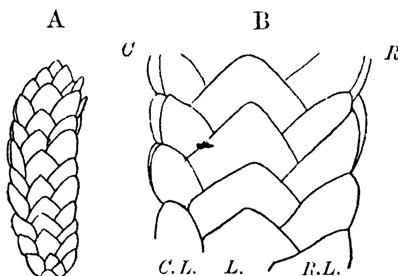


FIG. 58.

Turrilepas Wrightii. A, view of the whole fossil. B, a portion further enlarged. C, carinal scales; C.L, carino-lateral, L, lateral; R.L, rostro-lateral; R, rostral. (From Gruvel's *Monographie*.)

The number and arrangement of the calcareous plates on the outer surface of the body afford valuable systematic characters, throwing light on the phylogenetic history of the group. It seems probable that in the most primitive Cirripedia there was no distinction of capitulum and peduncle, the whole body being enveloped by a mantle, probably bivalved, and strengthened with shelly plates. Such a form is perhaps represented by the fossil *Turrilepas* (Fig. 58) from Silurian and Devonian rocks, in which the whole animal appears to be covered with imbricating scales arranged in transverse rows of five on each side. The genus *Loricula* (Fig. 59), appearing in the Lower Cretaceous, has been supposed to represent the next stage of evolution, showing the beginning of the differentiation between peduncular and capitular plates. In the peduncular region the arrangement of the plates is the same as in *Turrilepas*. At one end of the animal, several

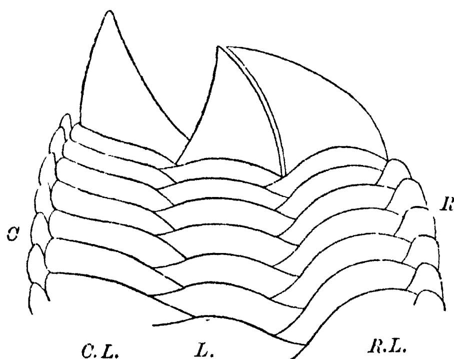


FIG. 59.

Loricula pulchella. C, carinal scales; C.L, carino-lateral; L, lateral; R.L, rostro-lateral; R, rostral. The capitular plates are not correctly shown. (From Gruvel's *Monographie*.)

plates of the terminal row on each side are much enlarged and represent the capitular plates. Much older than *Loricula*, however, and probably much more primitive, is the still-existing genus *Pollicipes*, which dates back to the Silurian, possibly to the Ordovician epoch. In *Pollicipes* the peduncle is covered with small scale-like plates which increase in size towards the capitular end, and in some cases (*P. sertus* (Fig. 60)) show a complete gradation of size and arrangement up to the capitular plates themselves. The latter consist of unpaired *rostrum* and *carina*, with paired *terga* and *scuta*, with a varying number of *lateral* plates, forming a transition to the scales of the peduncle.

From the type of *Pollicipes* two lines of modification may be

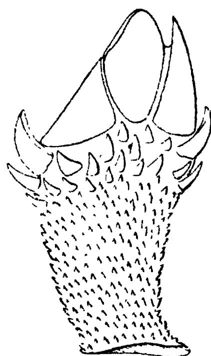


FIG. 60.

Pollicipes sertus, showing transition from peduncular scales to capitular plates. (From Gruvel's *Monographie*.)

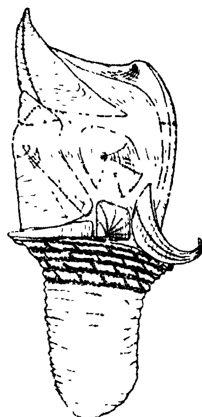


FIG. 61.

Scalpellum stearnsii, $\times \frac{2}{3}$. (After Stebbing, from *Encycl. Brit.*)

traced. On the one hand, in the group Pedunculata, we find the scales of the peduncle becoming horny and disappearing, while the capitular plates diminish in number as we pass from *Scalpellum* (Fig. 61), through forms like *Lepas* (Fig. 57, A) and *Dichelaspis*, to *Alepas* and *Anelasma*, where the mantle is entirely membranous.

On the other hand, the Operculata may be supposed to have originated from a form resembling *Pollicipes*, or intermediate between it and *Loricula*. The peduncle has disappeared, but the whorl of plates immediately below the capitular valves have persisted, and, together with the rostrum and carina, have become united to form the outer "wall" of tubular or conical form, within the opening of which the scuta and terga are articulated to form the movable operculum. The most primitive genus among the

Operculata is apparently *Catophragmus* (Figs. 62, 63), where the "wall" consists of eight pieces (or "compartments," as Darwin termed them), the unpaired rostrum and carina, and the paired lateral, rostro-lateral, and carino-lateral plates, and is further surrounded by several whorls of imbricating scales diminishing in size towards the periphery, and representing the armature of the vanished peduncle. In the other Operculata these scales are wanting, and a series can be traced in which the compartments diminish successively in number by coalescence, from *Octomeris*, which has eight plates, through *Balanus* (Fig. 57, B) with six, and *Elminius* with four, to *Pyrgoma*, where all the plates have coalesced and the "wall" is undivided. Each compartment presents three

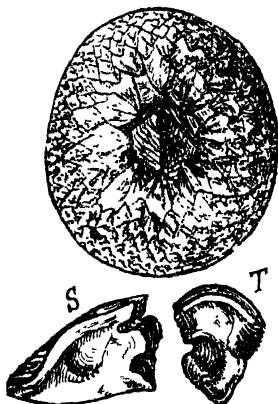


FIG. 62.

Catophragmus [illegible]. The upper figure represents the entire shell viewed from above. *S*, scutum; *T*, tergum, separated and further enlarged. (From Gruvel's *Monographie*.)

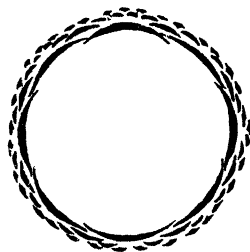


FIG. 63.

Diagram showing the constitution of the "wall" in *Catophragmus*. The eight principal compartments are surrounded by several whorls of scales. (From Gruvel's *Monographie*.)

divisions, a central *paries* flanked by two lateral portions known as *radii* or *alae* according as they overlap or are overlapped by the adjacent compartments. The exact manner in which the overlapping takes place varies in the different genera and affords a basis for systematic divisions. Thus Darwin divided his Balanidae into two sub-families: (1) the Chthamalinae, in which the rostrum has alae on both sides, or, in other words, is overlapped by the adjacent compartments; and (2) the Balaninae, in which the apparent rostrum is really formed by the fusion of the rostrum with the rostro-lateral compartments (Fig. 57, B, *r* + *rl*), and consequently has radii overlapping its neighbours on both sides. By some recent writers the arrangement of the plates is interpreted somewhat differently, and, though its phylogenetic importance is recognised, the classification adopted is made to rest upon the number of compartments distinct in the adult.

Generally included with the Operculata, though possibly deserving to rank as a separate sub-order, is the curious little group of Asymmetrica, comprising the single genus *Verruca*. These are sessile, like the true Operculata, and have the shell composed of a wall and closed by a movable operculum. But the operculum consists of the scutum and tergum of one side only, those of the other side being fused to form one-half of the wall, which is completed, on the side of the movable opercular plates, by the greatly developed and displaced rostrum and carina.

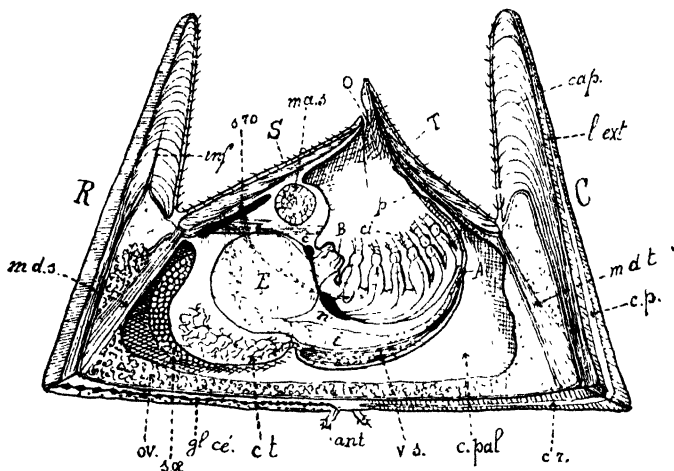


FIG. 61.

Diagrammatic vertical section of *Balanus*. The cirri are cut short. *A*, anus; *ant*, antennule; *B*, mouth; *C*, carina; *c*, cerebral ganglion; *cap*, lamellae of the "wall"; *ci*, cirri; *c.p*, parietal canal; *c.pal*, mantle-cavity; *c.r*, radial canal of the base; *c.t*, testicular caeca; *E*, stomach; *gl.ce*, cement-glands; *i*, intestine; *inf*, "infundibulum" (containing a prolongation of the mantle); *l.ext*, external lamina of the wall; *m.a.s*, adductor scutorum muscle; *m.d.s*, depressor scuti muscle; *m.d.t*, depressor tergi muscle; *n*, ventral nerve-mass; *o*, opening of mantle-cavity; *ov*, ovary; *p*, penis; *R*, rostrum; *S*, scutum; *s.oe*, egg-mass in mantle-cavity; *s.ro*, rostral blood-sinus; *T*, tergum; *v.s*, seminal vesicle. (From Gruvel's *Monographie*.)

In the Pedunculata the shell is formed of simple calcified plates, increasing in thickness by the application of successive layers on the inner surface, while the uncalcified cuticle between them scales off periodically to admit of growth, with the formation of a new cuticle underneath. In the simpler Operculata (*Chthamalus*), the compartments forming the wall are of this nature, but in most of the genera composing this group they have a more complex structure, being traversed by canals running parallel with the surface and containing prolongations of the hypodermis (Fig. 64, *c.p* and *inf*). The complexity of the shell reaches its maximum in the genus *Coronula*, the species of which attach themselves to the skin of whales. In these, the folding of the wall gives rise to

chambers on the inner and outer surfaces, receiving respectively branches of the ovaries of the Cirripede and prolongations of the epidermal tissue of the host.

The base of the shell in the Operculata may be simple and membranous or it may become calcified, and in the latter case it may be traversed by radial canals (Fig. 64, *c.r*) carrying prolongations of the hypodermis.

In *Xenobalanus* (Figs. 65, 66) among the Operculata the wall is reduced to a small vestige and the opercular plates are absent. The mantle-sac is elongated and appears as if divided into capitular and peduncular portions, giving the animal an extraordinarily close resemblance to certain Pedunculata such as *Alepas*.

It may be mentioned here that in the Pedunculate *Anelasma*, which is parasitic on sharks, the peduncle becomes imbedded in the muscles of the host and gives off minute ramifying filaments which no doubt serve for the absorption of nutriment.



Fig. 65.

Xenobalanus globicipitis. *B*, the reduced "wall"; *p*, penis. (From Gruvel's *Monographie*.)

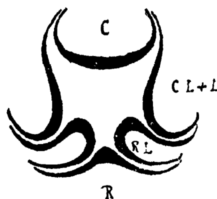


Fig. 66.

Diagram of the reduced "wall" of *Xenobalanus*. *C*, carina; *C.L+L*, carino-lateral fused with lateral; *R L*, rostro-lateral; *R*, rostrum. (From Gruvel's *Monographie*.)

The body, enclosed within the mantle, consists of a cephalic region ("prosoma" of Darwin), followed by a "thoracic" region corresponding to the somites bearing the six pairs of cirri. These somites are usually indistinctly defined in the membranous integument and the first is always coalesced with the head. There is no distinct "abdomen" in the adult except in so far as it is represented by the caudal furca which is present in most Pedunculata and a few Operculata. The furcal rami are usually small, unjointed or with few segments. Exceptionally they may be long and multiarticulate.

Appendages.—The *antennules*, which serve for attachment in the larva, usually persist in a functionless condition imbedded in the cement which fastens the end of the peduncle or the base of the

shell to the substratum (Fig. 64, *ant*, Fig. 67, *A'*). They appear, however, to be absent in the Acrothoracica.

The *antennae* disappear in the adult in all normal Cirripedia. Their possible persistence in the Ascothoracica will be referred to later.

The mouth-parts consist of simply formed *mandibles*, *maxillulae*, and *maxillae*, the last united at the base to form a lower lip. The upper lip is large, often bullate, and at the sides, between it and the mandibles, are a pair of setose lobes which have been sometimes interpreted as lateral lobes of the labrum, but which seem undoubtedly to be the mandibular palps.

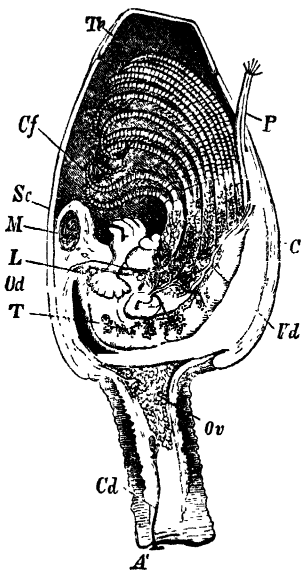


FIG. 67.

Dissection of *Lepas* from the side. *A'*, antennule; *C*, carina; *Cd*, cement-gland and duct; *Cf*, cirri (thoracic appendages); *L*, hepatic caeca; *M*, adductor muscle; *Od*, oviduct; *Ov*, ovary; *P*, penis; *Sc*, scutum; *T*, testis; *Tc*, tergum; *Vd*, vas deferens. (From Claus's *Textbook*).

The appendages of the "thoracic" region, of which there are normally six pairs, form the characteristic "cirri" from which the name of the order is derived (Fig. 67, *Cf*). Each consists of a two-segmented protopodite bearing two long multiarticulate rami, the segments of which are fringed with long hairs forming, when the cirri are protruded from the orifice of the shell, a "casting-net" for the capture of prey. The cirri increase in length and in the number of segments in the rami from before backwards, and the number of segments also increases with the age of the animal. The first pair are commonly, at least in the Pedunculata, separated by a little space from the following pairs, and more closely associated with the mouth-parts. Further, the first two or the first three pairs are distinguished from the posterior pairs by being shorter and by having the segments beset with stiff spines which probably aid in the prehension of food. In the parasitic *Anelasma* the cirri are short, obscurely segmented, and quite devoid of setae (Fig. 68).

In the Acrothoracica the cirri are reduced in number by the disappearance of the second and sometimes also of the third pair, and the first is separated by a wide space from the remaining pairs, which are crowded together at the posterior end of the body. The first pair are reduced to small papillae in *Cryptophialus*, but in the remaining genera they are closely approximated to the mouth-parts,

and have two unsegmented rami. In *Alcippe* the last three pairs of cirri are uniramous.

In many Pedunculata a membranous process ("filamentary appendage," Darwin) grows out from the side of the body just below the origin of the first cirrus. In *Conchoderma* similar appendages are also attached to the peduncles of some of the cirri, and in that genus and in *Pollicipes* others spring from the sides of the prosoma. These processes may be occupied internally by diverticula of the testes. In many Balanidae a setose plate is produced from the outer side of the peduncle of the third pair of cirri, and projects half-way across the dorsal surface of the body. In *Cryptophialus* two pairs of filamentary processes spring from the dorsal surface of the body. It seems possible that some of those appendages which are attached to the peduncles of the cirri or in the neighbourhood of their articulation to the body may be of the nature of epipodites. In many Cirripedia a fold of the integument projecting into the mantle-cavity originates on each side of the cephalic region at the point where the mantle joins the body. In the Pedunculata these folds, the "ovigerous frena" of Darwin, usually serve for the attachment of the egg-masses, and are equipped for that purpose with knobbed spines. In the Verrucidae they are absent, but in the other Operculata they are represented by large plicated membranes no doubt branchial in function.



Fig. 68.

Anelasma squalicola. One-half of mantle removed to show the body and the reduced cirri. (From Gruvel's *Monographie*.)

Alimentary System.—The stomodaeum appears, as a rule, to form only the narrow oesophagus, the large stomach being without a cuticular lining. In some Acrothoracica (*Cryptophialus*), however, a triturating apparatus is developed from the inner end of the oesophagus, where it enters the stomach, consisting of two opposed horny discs carrying teeth and several rows of setae. The anterior part of the stomach generally gives off a number of large "hepatic" caeca (Fig. 67, *L*), while ramifying tubules forming the so-called "pancreatic glands" clothe the posterior part and open into it by numerous small apertures.

In *Alcippe*, among the Acrothoracica, the rectum and anus are absent, and the ramified hepatic caeca radiate from the stomach into all parts of the body.

Circulatory System.—No heart is present in any Cirripede, and the lacunar channels in which the blood circulates are, for the most part, ill-defined. The most important and constant is the "rostral sinus" (Fig. 64, *s.ro*) lying on the rostral side of the adductor scutorum muscle. It has a pair of valves at its lower end where

it communicates, in the Pedunculata, with a canal traversing the length of the peduncle.

Excretory System.—The excretory organs of the Cirripedia have been the subject of much discussion, and it is only recently that their structure has been clearly ascertained. Darwin described as "olfactory" organs a pair of minute orifices, sometimes elevated on tubular papillae, on the outer side of the maxillae. These were shown by Hoek to be the openings of a pair of fine canals, which he regarded as "segmental organs" and described as opening into the body-cavity. This cavity has been shown by Bruntz to be the greatly enlarged "labyrinth" of the maxillary gland, the end-sac of which, discovered by Nussbaum, communicates with the labyrinth by a minute aperture. The end-sac is of considerable size, and may be divided by internal partitions. In addition to these maxillary glands, an excretory function is discharged by the hepatic caeca and by scattered "nephrocytes," the most important of which are aggregated in two masses at the sides of the cephalic region.

Glands.—A very peculiar and characteristic feature in the organisation of the normal Cirripedia is the cement apparatus by means of which the attachment of the animals is effected. This consists of a pair of much-ramified follicular glands connected with a pair of ducts which open, in the later larval stages at least, on the antennules. In the Pedunculata these glands are lodged in the peduncle (Fig. 67, *Cd*), and in the Operculata in the thickness of the basal plate (Fig. 64, *gl.ce*). In many Pedunculata (*Lepas*, *Conchoderma*, etc.) the openings of the ducts on the antennules serve throughout life for the escape of the cement, but in others (*Scalpellum*, *Pollicipes*) numerous additional apertures are formed on the surface of attachment. In the Operculata the glands and their ducts ramify in a complex way over the broad base and discharge the secretion through numerous pores. In one species of *Lepas* (*L. fascicularis*) the cement forms, at the end of the peduncle, a vesicular mass, serving to increase the buoyancy of the floating colony.

In the Acrothoracica, which bore into the shells of Mollusca and into corals, the cement-glands are much reduced and are probably functional only in early life.

Muscular System.—In the great majority of the Pedunculata and in the Operculata a strong adductor muscle (Fig. 64, *m.a.s*, Fig. 67, *M*) connects the two scuta dorsal to and in front (on the rostral side) of the alimentary canal. When the scuta are absent the muscle is attached on each side to the cuticle of the mantle. In the genus *Ibla* an *adductor scutorum* is also present, but as it crosses the body on the ventral side of the alimentary canal between the oesophagus and the ventral nerve-mass it cannot be regarded as homologous with the similarly named muscle of the

other Pedunculata and Operculata. In the Acrothoracica (*Alcippe*) also the adductor is ventral in position.

The peduncle of the Pedunculata is provided with longitudinal and oblique muscular fibres, and some of these may extend into the mantle, but no definite muscles other than the *adductor scutorum* are connected with the valves of the shell. In the Operculata Symmetrica, however (not in the Asymmetrica), a pair of *depressor* muscles are connected with the terga and two pairs with the scuta (Fig. 64, *m.d.t*, *m.d.s*).

Nervous System.—The ventral nerve-chain is concentrated into a single mass, within which, however, the outlines of five pairs of ganglia may be made out. In the Pedunculata a pair of large nerves originating from the anterior part of the cerebral ganglia pass down the peduncle, and may perhaps represent the antennular nerves.

Sense-Organs.—Apart from the setae, supposed to have a sensory function, on various parts of the external surface, and from such doubtfully sensory structures as "Koehler's organ" in the peduncular scales of *Pollicipes*, the chief organ of special sense persisting in the adult is the nauplius-eye. This is deeply buried in the tissues of the body, on the dorsal surface of the stomach, and may be single (Pedunculata), or divided into two parts (Operculata). In *Lepas* it consists of two pigment-cups, each containing a single (?) cell, the inner surface of which bears a series of rodlets imbedded in the pigment. The structure of the paired eyes in the Operculata is not fully known, but it seems probable that they correspond to the two halves of the Lepadid eye separated, and not to the paired compound eyes of the *Cypris* larva.

Reproductive System.—The great majority of the Cirripedia are hermaphrodite, and cross fertilisation is rendered possible by their gregarious habits.

The *ovaries* in the Pedunculata are lodged in the peduncle (Fig. 67, *Ov*), sometimes invading the mantle (*Conchoderma*), and in the Operculata they occupy the basal and, when fully developed, also the parietal portions of the mantle (Fig. 64, *ov*). The paired oviducts traverse the prosoma and open to the exterior at or near the base of the first pair of cirri. Just before reaching the exterior each oviduct expands to form a genital atrium (described by Darwin as an "acoustic organ"), with glandular walls within which is secreted a sac or sheath for the reception of the eggs. The extruded eggs contained in these sacs form the "ovigerous lamellae" frequently found within the mantle-cavity, where they are retained until hatching takes place.

The *testes* lie for the most part in the prosoma (Fig. 64, *c.t*, Fig. 67, *T*), extending, however, into the thoracic region and even into the filamentary appendages and the bases of the cirri.

Each vas deferens expands in the thoracic region to form a seminal vesicle (Fig. 64, *v.s*). The two vasa deferentia unite after entering the long thread-like penis (Figs. 64, *p*, and 67, *P*) which arises at the posterior end of the body on the ventral side of the anus. The penis can be protruded from the opening of the shell to deposit spermatozoa within the mantle-cavity of an adjacent individual, but probably self-fertilisation may occur in isolated individuals. The spermatozoa are filiform and motile.

Dwarf Males.—In the Operculata and in the great majority of the Pedunculata all the individuals of a species are similar and hermaphrodite, but in two genera of Pedunculata, *Scalpellum* and

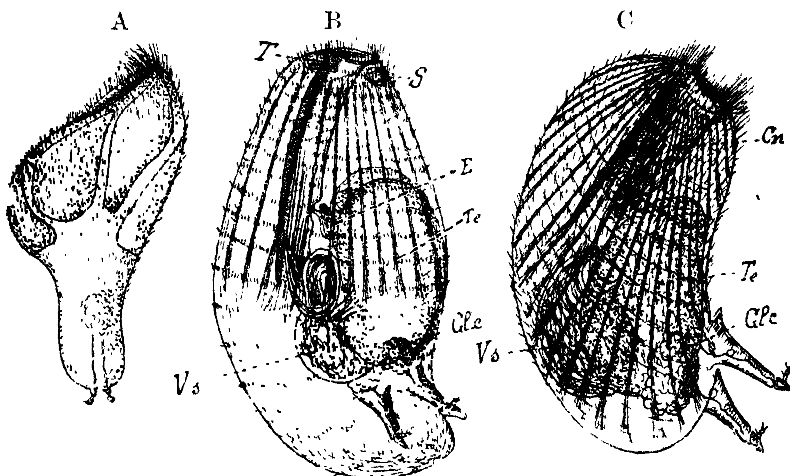


FIG. 69.

Dwarf males of—A, *Scalpellum peronii*; B, *S. gigas*; C, *S. velutinum*. *Cn*, vestige of mantle-cavity; *E*, stomach; *Gl.c*, cement-gland; *S*, scutum; *T*, tergum; *Te*, testis; *Vs*, seminal vesicle. (From Gruvel's *Monographie*.)

Ibla, dwarf male individuals occur. These are attached within the mantle-cavity of the large individuals, which may be either hermaphrodites of the usual type, or, in some cases, purely females. In the former case the males which are paired with hermaphrodite individuals present a type of sexual relations not definitely known to occur elsewhere in the animal kingdom except among the Myzostomida, and were termed by Darwin "complemental males."

As regards their structure, the dwarf males show great differences even in closely allied species of the same genus. In one group of species, including *Scalpellum peronii*, *S. villosum*, etc., the male is an almost perfect miniature of the large hermaphrodite to which it is attached (Fig. 69, A). The peduncle is distinct, though short, and the capitular plates are well developed. The

mouth-parts are normal, and the cirri are all present, but are composed of a restricted number of segments. The alimentary canal is complete, and in some cases even vestiges of the ovaries have been found. In a second group, comprising *S. vulgare*, *S. gigas*, etc., the peduncle and capitulum are no longer distinct, and the capitular plates are vestigial (Fig. 69, B). The mantle-cavity is greatly reduced, and the cirri are represented by six pairs of unsegmented processes each carrying two or three long setae. The gut ends blindly. In a third group of species, represented by *S. stromii*, *S. velutinum*, etc., the capitular plates have entirely disappeared and the structure is still further degenerate (Fig. 69, C). It is among the species of the third group that complete separation of the sexes occurs, the large individuals being quite devoid of male organs.

The degree of degeneration exhibited by the males appears to be correlated, to some extent, with their place of attachment to the female or hermaphrodite individuals. The less-modified males are lodged in fossettes in the margin of the mantle, while in those species where the modification is more profound the males are attached within the mantle-cavity below or behind the adductor muscle.

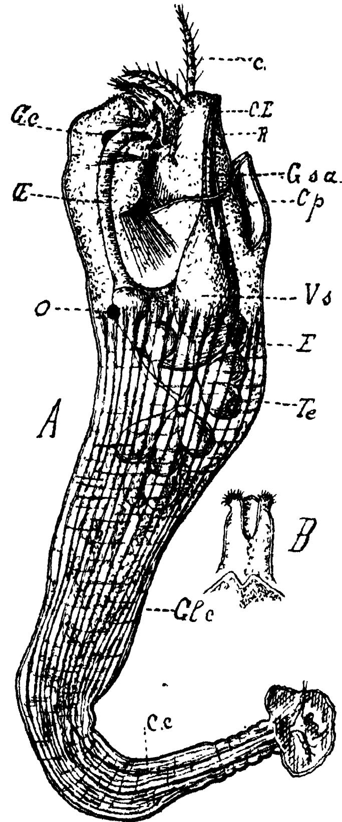


Fig. 70.

A, dwarf male of *Ibla quadrivalvis*. *Cc*, duct of cement-gland; *C.E*, terminal part of vas deferens; *Cp*, reduced mantle-cavity; *E*, stomach; *G.c*, brain; *Gl.c*, cement-glands; *G.s.o*, sub-oesophageal ganglion; *O*, eye; *Œ*, oesophagus; *R*, rectum; *Te*, testis; *V.s*, seminal vesicle; *c*, cirrus of last pair. B, posterior end of body with caudal furca. (From Gruvel's *Monographie*.)

In *Ibla* the male (Fig. 70) is modified in a manner somewhat different from that observed in *Scalpellum*. The peduncle is long and the mantle is greatly reduced and does not enclose the body. The mouth-parts are normal, but there are only two pairs of uniramous cirri. The alimentary canal is complete. The penis is short, in correlation probably with the length and flexibility of the peduncle and also with the place of attachment of the males,

which are lodged quite inside the pallial cavity, on the dorsal side of the body. Of the two species composing the genus *Ibla*, one, *I. quadrivalvis*, has hermaphrodite individuals (Fig. 71) with complemental males, while the other, *I. cumingii*, has the sexes separate.



FIG. 71.
Ibla quadrivalvis. (From Gruvel's *Monographie.*)

The males of the Acrothoracica (Fig. 72) are still further modified. The appendages and alimentary canal are quite wanting and the mantle forms merely a sheath for the greatly developed penis, which, in *Alcippe*, can extend to three or four times the length of the body. These anenterous males must of necessity be short-lived, and in addition to the two to fourteen males which are attached to the mantle margin of a single female, there will often be found the remains of the adhering antennules of several others which have attached themselves and died since the last moult of the female.

There can be but little doubt that hermaphroditism is the primitive condition among the Cirripedia, though

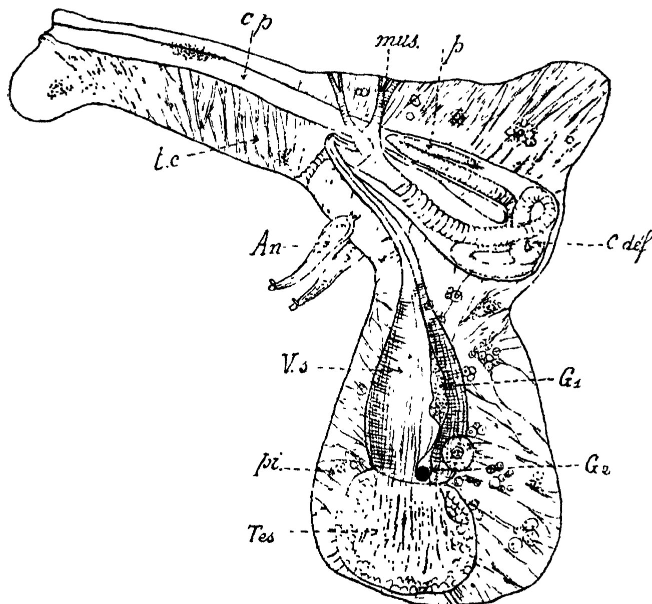


FIG. 72.

Dwarf male of *Alcippe lampas*. *An*, antennules; *C.def*, vas deferens; *C.p*, canal of the penis (vestige of mantle-cavity); G_1, G_2, nerve-ganglia; *mus*, retractor muscles of the penis; *p*, penis; *pi*, pigment; *Tes*, testis; *t.c*, connective tissue; *V.s*, seminal vesicle. (After Berndt, from Gruvel's *Monographie*.)

the reverse is probably the case with regard to the class Crustacea as a whole. It has been held by some authorities that the dioecious state is the more primitive in the Cirripedia also, and the attempt has been made to show that the more degraded types of the dwarf males resemble in their structure the *Cypris* larva, which is supposed to represent the ancestral form of the Cirripedes before the assumption of the sedentary habit. As a matter of fact, however, the points of resemblance between these males and the *Cypris* larva are very slight. Such characters as the incomplete alimentary canal and the reduced cirri show that these males are not primitive but degenerate forms, and that a phylogenetically older stage is represented by species like *S. peronii*, in which the males resemble the hermaphrodite individuals. It is very probable that the differentiation of the sexes began among species in which, on account of their deep-sea habitat (as in most species of *Scalpellum*) or burrowing habits (as in the Acrothoracica), cross-fertilisation between hermaphrodites was difficult. It is common, in many species of Pedunculata, to find young individuals attached to the peduncle of older ones, and it is but a step further to find these younger individuals, attached in the most favourable position for fertilisation to the mantle-margin of the others, performing only the function of males. It is more difficult, perhaps, to imagine why in so few cases is the separation of the sexes complete, but possibly the retention of male organs by the large individuals may be regarded as a precaution against a failure in the succession of short-lived males.

Development.

With a very few exceptions, the Cirripedia are hatched from the egg in the nauplius stage, and all pass through a later larval form, known, from the superficial likeness of its bivalved shell to that of an Ostracod, as the *Cypris* stage. The nauplius (Fig. 73) has a somewhat peculiar and characteristic structure, subject, for the most part, to but slight modification in the different groups. The dorsal shield is produced at the antero-lateral corners into a pair of tubular horns, sometimes of great length. Each horn has, at its base, a pair of unicellular glands (Fig. 73, *dr*) which discharge their secretion through its open tip. The posterior end of the shield is rounded, at least in the earlier stages, but immediately beneath it arises a long spine directed backwards. A large process projecting downwards and backwards from the ventral surface contains, in the later stages of development, the rudiments of the trunk and its appendages. It must therefore be regarded as the posterior end of the body, and the fork which terminates it must be compared with the "caudal furca," although the anal opening (*A*) is well in front of it on the dorsal side. The usual three pairs of limbs present the character-

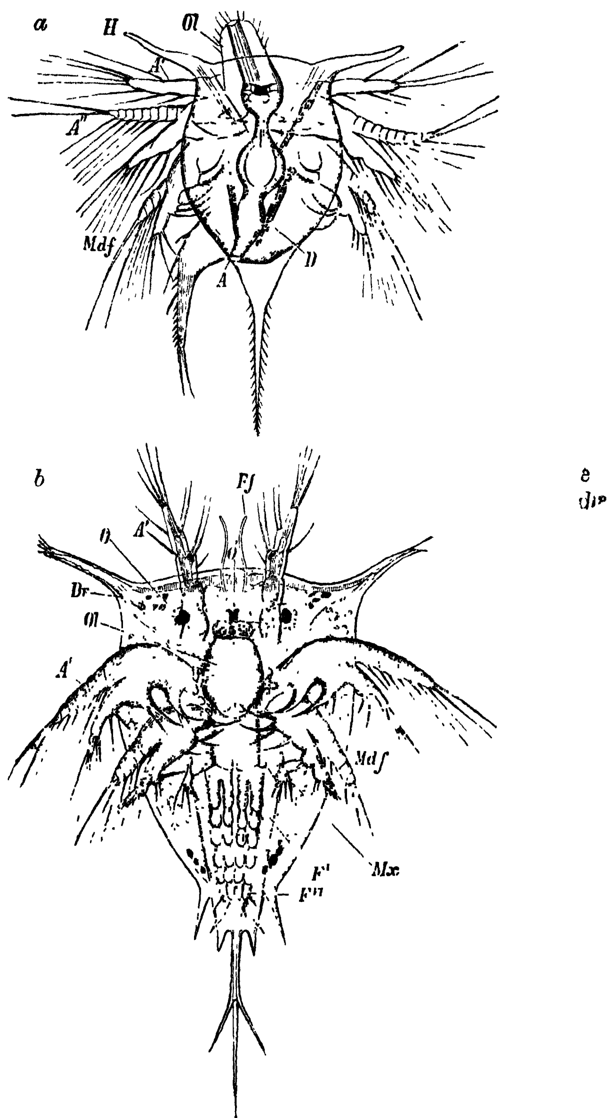


FIG. 73.

Larval stages of *Balanus*. *a*, late nauplius stage; *b*, metanauplius, just about to pass into the *Cypris* stage; *A*, anus; *A'*, antennule; *A''*, antenna; *D*, intestine; *Dr*, fronto-lateral gland; *F*i-*F*vi, the six thoracic appendages of the *Cypris* stage beneath the cuticle of the metanauplius; *Ff*, frontal filament; *H*, fronto-lateral horn; *Mdf*, mandible; *Mx*, maxillula; *O*, paired eye of *Cypris* stage; *O'*, nauplius-eye; *Ol*, upper lip, turned forward in *a*. (From Claus's *Textbook*.)

istic nauplius structure. In the second and third pairs the exopodite is multiarticulate and beset with natatory setae, and the protopodite has masticatory hooks. The mouth is overhung by a labrum (*Ol*) which in its great size recalls the corresponding organ of the Branchiopod nauplius. It contains a group of gland-cells which open at its tip. The unpaired eye (*O′*) is always well developed, and after the first stage a pair of sensory "frontal filaments" appear. The later nauplius stages are characterised, especially in the Pedunculata, by the development of spine-like processes from the dorsal shield and by the elongation of the caudal and posterior dorsal spinous processes of the body. A spine which develops from the middle of the dorsal shield was regarded by Dohrn as representing the mid-dorsal spine of the Brachyuran zoëa. Six pairs of movable spinules are commonly developed in the later stages on the ventral surface of the caudal process, and these have been regarded as corresponding to the rudiments of the six pairs of thoracic limbs. However this may be, the series of nauplius stages is closed with a definite metanauplius stage (Fig. 73, *b*), in which a rudiment of the fourth pair of appendages (maxillulae) is present. In this stage a downward flexure of the lateral portions of the dorsal shield is observed foreshadowing the development of a bivalve shell which encloses the body in the succeeding *Cypris* stage. The six pairs of thoracic limbs (F^{i}, F^{vi}) can be seen developing under the cuticle, as can also the adhesive disc of the antennules and the paired compound eyes.

At the next moult the larva passes at once into what is known as the *Cypris* stage (Fig. 74). The presence of a large bivalve shell gives it a general resemblance to one of the Ostracoda, but it must be noted that this resemblance does not extend to the number or structure of the limbs nor to the internal anatomy. All the appendages of the adult are present, and the larva is now essentially a free-swimming Cirripede. The mouth is closed, and the stage was styled by Darwin a "locomotive pupa." The two valves of the shell are continuous in the mid-dorsal line, and the free ventral margins show a certain asymmetry as in many Ostracoda. An adductor muscle in the same position as in the adult serves to bring the valves together. Near the anterior end on the ventral margin of each valve is a minute aperture which in some cases (*Lepas pectinata*) is elevated on a blunt horn-like process. In connection with this opening is a gland which is probably to be identified with the gland of the fronto-lateral horn in the nauplius stage. The antennules (Fig. 74, 1) are protruded between the valves of the shell anteriorly. The third segment is expanded into a sucker-like disc, on which opens the duct of the cement-gland, and which serves for the occasional temporary attachment of the larva. The terminal segment is attached to the side of the third, and bears besides

several setae a large olfactory filament or "aesthetasc." The antennae are reduced to shapeless vestiges and soon disappear entirely. The labrum becomes greatly reduced in size. The mandibles are represented only by the gnathobasic portion, the rest of the limb being reduced to a papilliform "palp." The maxillulae and maxillae are closely crowded together in nearly the position which they occupy in the adult, and form, with the mandibles and labrum, a prominent buccal mass. At this stage all the mouth-parts are devoid of setae and are not functional. The six pairs of thoracic limbs are now well developed. Each consists of a protopodite of two segments and two rami, each also bi-segmented, carrying long natatory setae. The "thoracic" region of the body is indistinctly segmented, and is followed by a small limbless

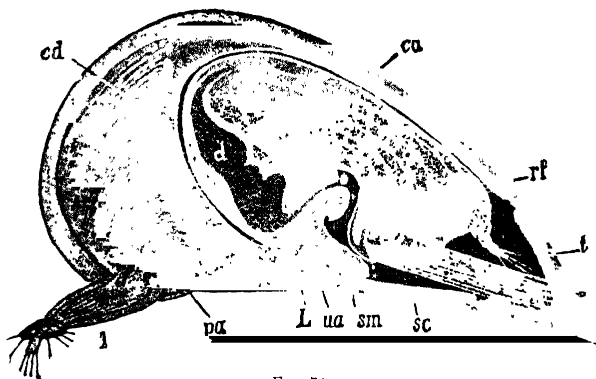


Fig. 74.

"Pupa" (late *Cypris* stage) of *Lepas pectinata*. *ca*, carina; *cd*, cement-gland; *d*, alimentary canal; *L*. hepatic diverticulum; *o*. mouth; *pa*, paired eye; *rf*, thoracic limbs, with the cirri of the adult developing inside; *sc*, scutum; *sm*, adductor muscle; *t*. tergum; *ua*, nauplius-eye; 1. antennule, with adhesive sucker. (After Claus, from Korschelt and Heider's *Embryology*.)

abdomen of four segments terminating in a short setose caudal fork.

As regards the internal anatomy, the unpaired eye (*ua*) persists and is accompanied by a pair of large compound eyes (*pa*) which were already visible in the last metanauplius stage. Paired diverticula from the anterior portion of the alimentary canal form the rudiments of the digestive gland, and a rudiment of the ovary is also visible in the anterior region. Finally, the *Cypris* larva becomes permanently attached by means of the antennules, and considerable changes go on under the cuticle in preparation for the next moult.

The most important of these changes (Fig. 75, A, B) are the development of the long cirriform thoracic limbs of the adult, and a concomitant change in the position of the thoracic region of the body which comes to lie at right angles to the long axis of the

shell. A deep fold of the integument (*y*) is formed on the ventral surface of the preoral region. At the next moult this fold becomes opened out, and the ventral surface posterior to it, which was at first in contact with the surface of attachment, becomes erected at right angles to this surface (Fig. 75, C). In this way the peculiar form of body characteristic of the adult Cirripede is attained. In the Pedunculata the stalk is developed by the elongation of the preoral region of the head. The compound eyes are cast off with the *Cypris* cuticle, and the rudiments of the five primary valves of the shell (scuta, terga, and carina) are developed.

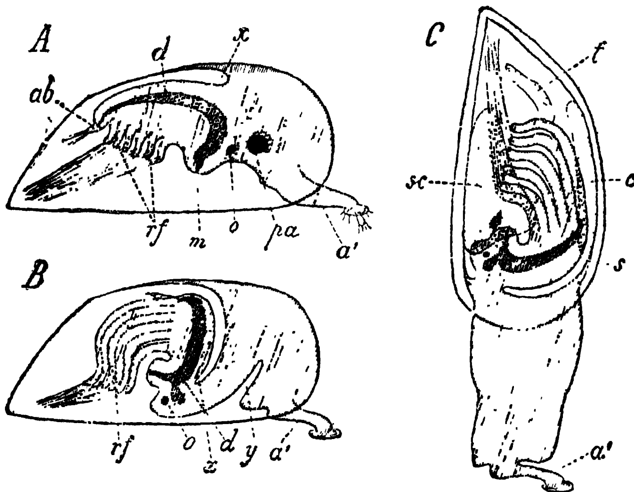


Fig. 75.

Diagram illustrating the metamorphosis of *Lepas*. A, *Cypris* stage. B, attached larva. C, young *Lepas*, still surrounded by the loosened *Cypris* shell (*s*) *a'*, antennule, *ab*, abdomen; *c*, carina; *d*, alimentary canal; *m*, mouth; *o*, nauplius-eye; *pa*, paired eye; *rf*, thoracic limbs; *s*, *Cypris* shell; *sc*, scutum; *t*, tergum; *x*, dorsal fold; *y*, ventral fold. (From Korschelt and Heider's *Embryology*.)

Morphology of Ascothoracica.

In the Ascothoracica, all of which are parasitic in Zoantharia or Echinoderma, the mantle may have a bivalved form (*Synagoga* and *Petrarca*), or it may form a capacious sac (*Laura*, Fig. 76) much larger than the body, with which it is connected by a narrow neck, and having only a small opening to the exterior. In *Dendrogaster* (Fig. 78) the mantle is still more developed, and is produced into branched lobes. In *Laura* the mantle is covered with stellate papillae penetrating the tissues of the host, and presumably absorptive. In all cases the mantle contains ramifications of the enteric diverticula and portions of the gonads. The body

in *Laura* (Fig. 77) is distinctly segmented into six "thoracic" and three limbless "abdominal" somites, and ends in a caudal furca. In *Petrarca* and *Dendrogaster* the body is unsegmented.

In the three genera just named a pair of preoral appendages are present (Fig. 77, *ant*) and, except in *Laura*, are armed with hooked spines suggesting that they are organs of fixation. They differ from the adhering antennules of the Thoracica and Acrothoracica in being inserted, at least in *Laura*, at the sides of the buccal region and more or less enveloped by the mantle. It is possible that they are in reality the antennae, but there seems to be no definite evidence

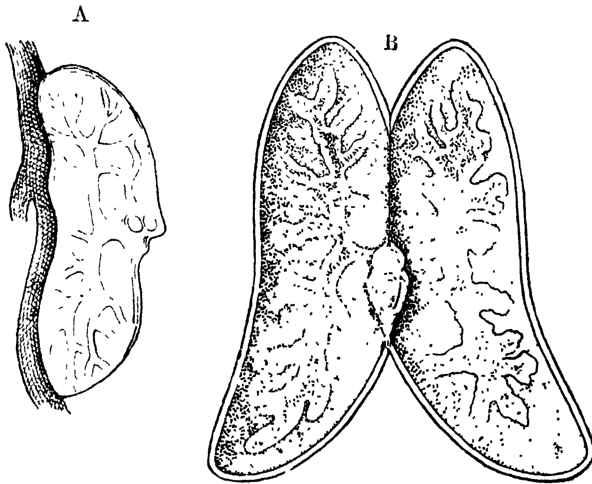


Fig. 76.

Laura gerardiae. A, external view of the animal attached to a branch of the coral *Gerardia* (soft tissues of coral removed). B, the mantle-sac split open showing the body in the middle. The ramified hepatic diverticula, which are accompanied by branches of the ovary, are seen in the mantle on each side. (After Lacaze-Duthiers, from *Encycl. Brit.*)

on the point. The cement-glands, so characteristic of other Cirripedia, appear to be absent.

The mouth-parts are more or less reduced, but appear to be adapted for piercing.

The thoracic appendages are biramous and articulated only in *Synagoga*. In *Laura* they are uniramous and indistinctly segmented, and the first pair differs from the others, being long and slender. A similar difference is observed in *Petrarca*, where, however, they are still further reduced, and in *Dendrogaster* they are represented only by some indistinct papillae.

In all three genera the gut ends blindly, and the hepatic diverticula (Fig. 76, B; Fig. 77, *F*), which are large, extend into the mantle. A digastric "adductor" muscle is present on the

ventral side of the alimentary canal. The nervous system is reduced. An eye is stated to be present in *Synagoga*. In *Laura* the oviducts open at the base of the first pair of cirri. In the other genera they have not been traced. *Petrarca* is hermaphrodite, and the vasa deferentia open on a large penis which terminates the body. In *Laura* the testes are described as lodged in the bases of the second, third, fourth, and fifth cirri, opening to the exterior by numerous fine ducts, but this account is open to doubt. Dwarf males have recently been described in *Dendrogaster*.

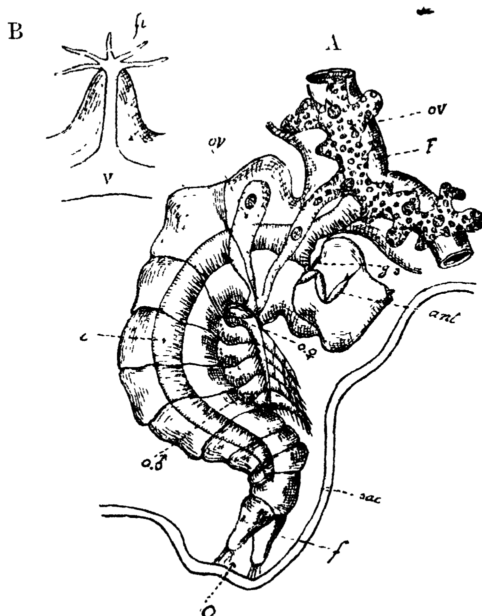


FIG. 77.

Laura gerardiae. A, body exposed by removal of one-half of the mantle. *ant*, antenna; *F*, hepatic diverticula; *f*, caudal furca; *g.s*, cerebral ganglion; *i*, intestine; *o*, opening of mantle; *ov*, ovary; *o.* ♀, opening of oviduct; *o.* ♂, opening of male ducts; *sac*, wall of mantle. B, one of the papillae of the mantle. *fi*, vascular filaments; *v*, blood-vessel. (After Lacaze-Duthiers, from Gruvel's *Monographie*.)

A nauplius larva peculiar among the Cirripedia in lacking the fronto-lateral horns of the carapace has been observed in *Laura*. In *Dendrogaster* the nauplius stage is suppressed and the larva hatches as a peculiar *Cypris* larva (Fig. 78, C), with only five pairs of biramous thoracic limbs, a long abdomen of five somites, stout antennules with hooks, and a very large olfactory filament (aesthetasc). There are no eyes, and the gut already sends a diverticulum into each valve of the shell.

Morphology of Apoda.

This order was established by Darwin for the reception of a single species, *Proteolepas bivincta*, of which he found a solitary specimen parasitic within the mantle-cavity of a pedunculate Cirripede, *Alepas cornuta*, from the West Indies. No further specimens have been seen by later investigators.

Proteolepas (Fig. 79) is referred to the Cirripedia mainly because it possesses adhering antennules which agree minutely with those of

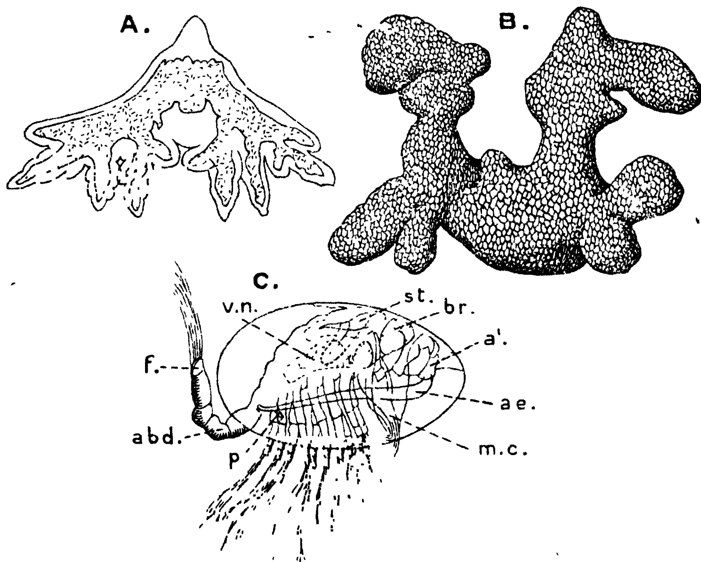


Fig. 78.

Dendrogaster astericola. A, young specimen; B, older specimen; C, *Cypris* larva. *a'*, antennule; *ae*, aesthetasc; *abd*, abdomen; *br*, supra-oesophageal ganglion; *f*, caudal furca; *m.c*, mouth-cone; *p*, rudiment of penis; *st*, stomach, sending a diverticulum into the shell-valve; *v.n*, ventral nerve-mass. (After Knipowitsch.)

normal Cirripedes. It differs most conspicuously in the absence of any trace of a mantle and of thoracic limbs.

The body is elongated and maggot-like. It is divided into eleven segments, but as one of the segments is in front of that bearing the antennules, it seems clear that this segmentation does not express the number of true somites present. The mouth-parts, borne on the first "segment," seem to be adapted for piercing and sucking. The labrum partly ensheathes the gnathites, of which there appear to be two pairs, turned outwards, and serrated on the outer margin. From the dorsal surface of the second segment

proceed two ribbon-like filaments (Fig. 79, A, *ant*), bearing at the tip the larval antennules, which agree in structure, as already noticed, with the type usual among normal Cirripedes. The six following "segments" were regarded by Darwin as thoracic and the three remaining as abdominal. All of them are devoid of any trace of appendages.

The alimentary canal is greatly reduced. According to Darwin, only the oesophagus is present, and there is no trace of stomach, rectum, or anus. The ovaries lie at the sides of the anterior part of the body and the testes posteriorly. The vasa deferentia unite to open at the tip of the abdomen. There is no penis.

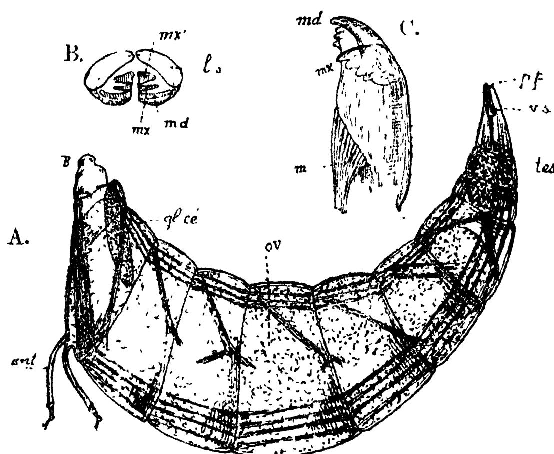


FIG. 79.

Proteolepas bivincta. A, the entire animal; *ant*, antennules; *B*, buccal cone; *gl.ce*, cement-gland; *p.p*, penial papilla; *tes*, testis; *v.s*, seminal vesicle. B, diagrammatic plan of mouth-parts; *l.s*, upper lip, *md*, mandible; *mx*, maxillula; *mx'*, maxilla. C, mandible and maxillula separated; *m*, muscle. (After Darwin, from Gruvel's *Monographie*.)

While Darwin was unable to investigate the development of the species, Hansen has recently conjecturally referred to the Apoda certain nauplius larvae obtained in various parts of the Atlantic Ocean and the Baltic, while more recently similar larvae have been found in the Adriatic Sea. In late nauplius stages of this type rudiments of paired compound eyes and of six pairs of thoracic limbs are visible, so that it can hardly be doubted that they belong to some form of Cirripede. On the other hand, they differ markedly in the absence of antero-lateral horns and of frontal filaments, in the shape of the body, and especially of the strongly developed dorsal shield, and in other characters from the known Cirripede larvae, which, as already indicated, show great uniformity

of structure throughout the group. After a careful discussion of all their characters, Hansen considers that they must in all probability belong to the Apoda, and he considers that the material examined by him includes at least ten species.

Morphology of Rhizocephala.

The Rhizocephala are an exclusively parasitic group, nearly all infesting Decapod Crustacea, and are distinguished from the normal Cirripedes by the complete loss in the adult state of all

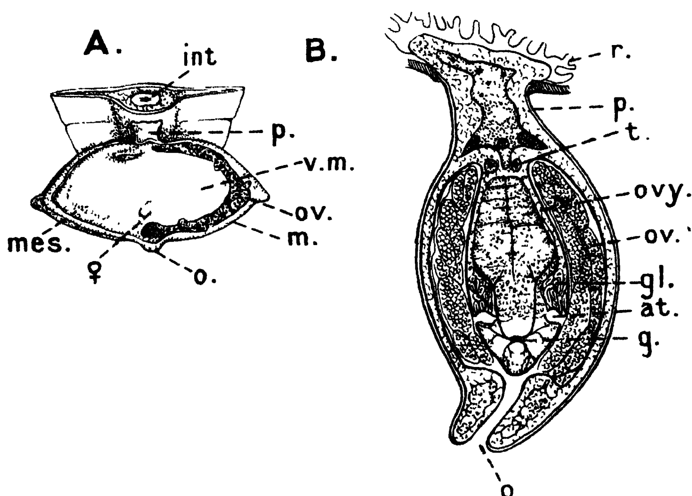


Fig. 80.

A, *Sacculina carcini* in position on the detached abdomen of the crab; one side of the mantle has been removed. *int*, intestine of the host, surrounded by the roots of the parasite; *m*, mantle; *mes*, mesentery; *o*, opening of mantle-cavity; *ov*, egg-masses in mantle-cavity; *p*, peduncle; *v.m*, visceral mass; ♀, opening of genital atrium, the outline of the colleteric gland is seen surrounding it. The outline of the testis is seen above, a little to the left of the peduncle. B, vertical section of *Sacculina* at right angles to the plane of the mesentery (semi-diagrammatic); *at*, genital atrium; *g*, nerve-ganglion; *gl*, colleteric gland opening into genital atrium; *ovy*, ovary; *r*, absorptive roots; *t*, testis; other letters as in A. (After Delage.)

traces of segmentation and of appendages, and (excluding for the present the doubtful *Sphaerothylacus*) by the absence at all stages of life of an alimentary canal.

The body (Fig. 80, A) has the form of a simple sac attached by a short peduncle, from which root-like processes ramify throughout the body of the host. These absorptive roots appear to be absent in the aberrant genus *Duplorbis*. The visceral mass, or body proper, is completely enveloped by the mantle, which has a narrow aperture (*o*) capable of being closed by a sphincter muscle. In *Sylon* the opening is double, and in *Clistosaccus* and *Duplorbis* the mantle-cavity is completely closed. The mantle is attached to the

visceral mass by a narrow mesentery (*mes*), near to which on each side are the paired (more rarely unpaired) openings of the male and female generative organs. In the different genera the external form varies considerably, and with it the position of the mesentery and of the genital apertures. In *Peltogaster* (Fig. 81, B), which may be regarded as the most primitive form, the body has an elongated sausage-shape, with the mantle-opening at one end, and is attached by the peduncle about the middle of its length. The mesentery is longitudinal on the proximal side (next the peduncle). The genital apertures are placed on each side close to the mesentery, the female openings being nearer the end where the opening of the mantle is situated. Comparison with a normal Cirripede (Fig. 81, A), especially as regards the position of the genital apertures, suggests that the mesentery is on the *dorsal* side, and the mantle-

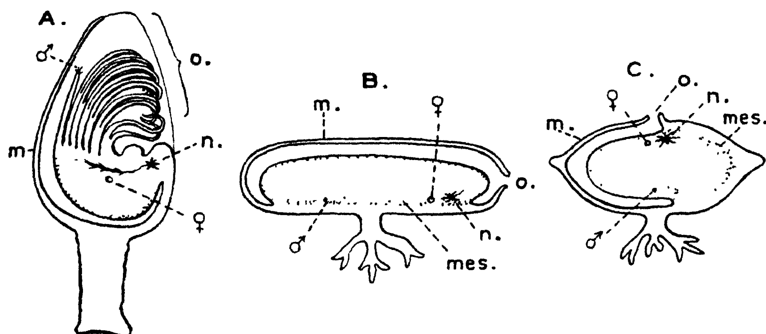


FIG. 81.

Diagram to illustrate comparison of Rhizocephala with normal Cirripede. A, *Lepas*; B, *Peltogaster*, C, *Sacculina*. *m*, mantle; *mes*, mesentery; *n*, nerve-ganglion; *o*, opening of mantle-cavity. ♂, male generative aperture; ♀, female generative aperture.

opening at the anterior (or rostral) end. In *Sacculina* (Fig. 81, C), which is parasitic on Brachyura, the whole body is flattened in the plane of the mesentery, and has assumed a secondary and superficial bilateral symmetry about a plane at right angles to this and coinciding with the median plane of the host. The mantle-aperture is in the middle of the distal edge, and the mesentery has suffered a corresponding displacement, extending from the mantle-opening to the point of attachment of the peduncle on the side which, in the natural position, is turned towards the right side of the host. The genital openings, except that they are more widely separated from each other, occupy the same relative positions as in *Peltogaster*. In other genera, such as *Lernaeodiscus* and *Triangulus*, the symmetry becomes still more complicated, and in *Clistosaccus* and *Sylon* the genital organs are unpaired.

The peduncle perforates the integument of the host and gives

off on the inside the absorptive roots which, in the case of *Sacculina*, penetrate into all the organs of the host, with exception of the gills and the heart, and extend to the terminal segments of the legs and into the antennules and eye-stalks. The roots are covered by a very delicate cuticle, beneath which is a layer of hypodermic cells, and the interior is occupied by reticular connective tissue, only the larger trunks having a central cavity. At the tips of the rootlets in *Sacculina* the outer layers are invaginated to form a cavity known as the "lagena." In the genus *Duplorbis*, where the root-system appears to be absent, the peduncle is hollow, its cavity communicating with the closed mantle-cavity and opening at the other end into the body-cavity (haemocoel) of the host.

Internal Anatomy.—Apart from a single nervous ganglion (Fig. 80, B, *g*) which lies close to the mesentery near the female genital openings, the only organs present are those of the generative system. The ovary (*ovy*) is divided into two much-lobed masses united by a median portion and giving off on each side a short oviduct, which widens into a "genital atrium" (*at*) before opening into the mantle-cavity. The walls of this atrium, as in the normal Cirripedes, are glandular, often growing out into branched tubular glands (*gl*) ("colleteric" glands) supplying the material of the envelopes within which the eggs are packed in the mantle-cavity. In *Sacculina* the egg-masses are retained in position by barbed spines ("retinacula") grouped on papillae on the lining membrane of the mantle.

The testes (*t*) have each the form of an elongated sac narrowing towards a short vas deferens. The spermatozoa are filiform and actively motile.

F. Müller was the first to suggest that the *Cypris* larvae, which, as Lilljeborg had previously observed, are often found attached near the mantle-opening of young specimens of *Peltogaster*, might be complemental males. Delage accepted this interpretation for the larvae which he observed in the same position in *Sacculina*, but he was unable to obtain them alive or to observe any trace of male organs. At this stage the mantle-opening is still closed by a plug of chitin, and it is difficult to see how fertilisation could be effected. G. Smith, who has recently investigated the subject, finds that the larvae die very soon after they become attached, without developing further. In only one instance did he find evidence of what seemed to be an abortive attempt of the cellular contents of the larva to pass into the tissues of the mantle in the way in which the contents of the larvae pass into the host in the ordinary course of development. G. Smith believes the attachment of these larvae to be an atavistic phenomenon; that the larvae are, in fact, vestigial male individuals. The same observer has found in the mantle-cavity of

Duplorbis what appear to be extremely degraded, but still functional male individuals. In this genus the usual testes are absent, as they are also in *Sylon*, but in the latter no male individuals have been found, and parthenogenesis may perhaps occur.

Development of Rhizocephala.

The development has been most fully worked out in the case of *Sacculina* by Delage, whose results have been confirmed and extended by G. Smith. The larva is hatched in the form of a nauplius (Fig. 82, A) showing a general resemblance to that of the normal Cirripedes, but differing in having no alimentary canal. The fronto-lateral horns are well developed and each contains a pair of gland-cells (*gl*). A process on the ventral side, called by Delage the rostrum, appears to represent the labrum, but there is no mouth. Posteriorly the body terminates in a caudal furca. The three pairs of limbs have the usual form, but the second and third pairs are without the masticatory hooks found in the normal Cirripedes. Frontal filaments (*fs*) are present, as is also the unpaired eye (*ua*) resting on a cerebral ganglion. In the later stages the thoracic somites and their appendages become differentiated within the posterior part of the body, not forming a postero-ventral process as in the normal Cirripedes.

The *Cypris*-stage (Fig. 82, B) agrees in all essentials with that of the normal Cirripedes except for the absence of a mouth and alimentary canal, and the vestigial condition of the mouth-parts. The fronto-lateral glands (*gl*) open in the usual position near the margin of the valves of the shell. The antennules consist of three segments only, and are without any adhesive disc; the terminal segment bears two appendages which are probably sensory and a backwardly curved filamentous process which is stated to be the organ of attachment. The six pairs of thoracic limbs have the protopodite not distinctly segmented and the exopodite and endopodite each composed of two segments. The abdomen (*ab*) is unsegmented and terminates in a pair of furcal appendages. The unpaired eye persists, but beyond the muscles for moving the body and appendages no other internal organs are differentiated. It is worthy of note that there appear to be no cement-glands in connection with the antennules.

After a free-swimming life of three or four days, the *Cypris* larva becomes attached to the host. In the case of *Peltogaster*, which infests hermit-crabs, it is probable that the larva settles at or near the spot where the adult afterwards appears on the host's abdomen. In *Sacculina*, which attacks Brachyurous crabs, however, the place of attachment of the larva has no relation to the place of emergence of the adult parasite, the latter being always found under

the crab's abdomen in a position inaccessible to the larva. As a rule, the crab is attacked when the integument is still soft after ecdysis, and the larvae may attach themselves at any point on the dorsal surface of the carapace or on the limbs, at the base of one of the large setae where the articular ring of uncalcified cuticle allows

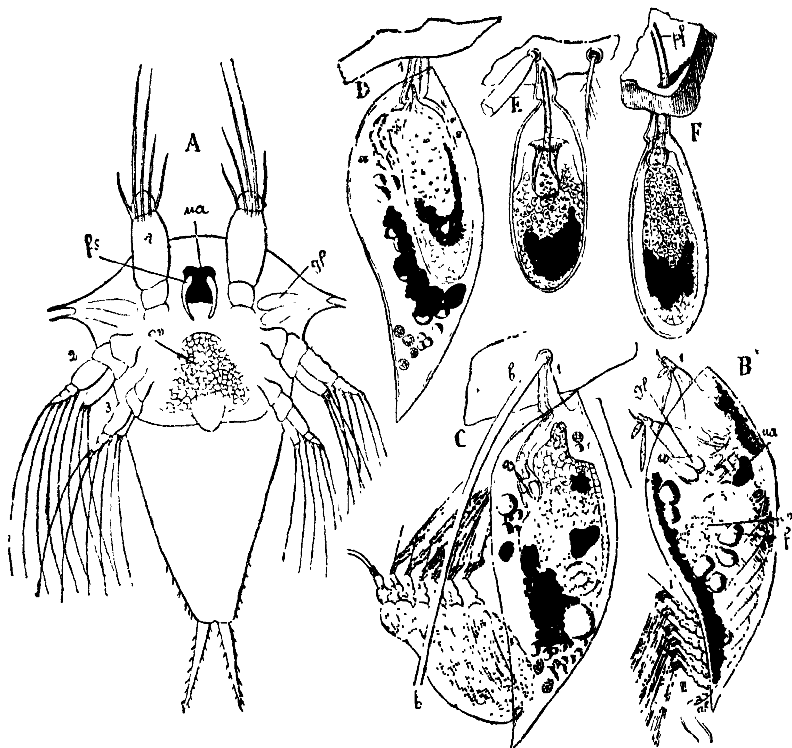


FIG. 82.

Larval stages of *Sacculina carcini*. A, nauplius after the first moult. B, free-swimming *Cypris*-stage. C. *Cypris*-stage after attachment to a seta (*bb*) of the host. D, formation of the *Kentrogon* larva. E, *Kentrogon*-stage, after the *Cypris* shell has been cast off and the "dart" has been formed. F, penetration of the dart through the cuticle of the host. 1, 2, 3, the three pairs of nauplius-limbs. I-VI, thoracic limbs. *ab*, abdomen; *bb*. seta of the host; *f*,' fat-globules; *f.s*, frontal sense-organ; *gl*, glands of the antero-lateral horns: *ov*, mass of mesoderm cells regarded by Delage as the rudiment of the ovary; *pf*, "dart"; *ua*, nauplius-eye. (After Delage, from Korschelt and Heider's *Embryology*.)

more easy penetration (Fig. 82, C). Only one of the antennules is used for attachment, the filamentous process of the terminal segment clasping the base of the hair. The whole of the thoracic region of the larva, with its appendages and muscles, now becomes detached and is thrown off, and later the bivalve shell is also shed, while the contents of the anterior region of the body become

retracted and enclosed in a new cuticle, remaining connected only with the antennule which is fixed to the host (Fig. 82, D). Within the sac thus formed, a tubular chitinous organ known as the "dart" becomes differentiated. At first the dart is invaginated into itself, and in connection with it a second cuticular sac becomes separated within the first. The larva at this stage was designated by Delage the "Kentrogon" (Fig. 82, E). The point of the dart lies within

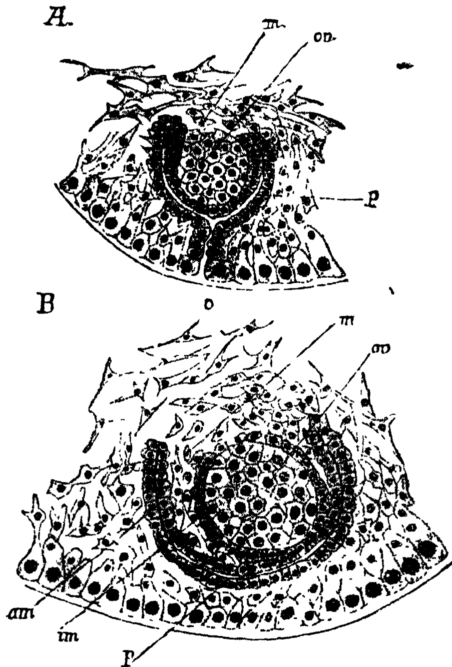


Fig. 83.

Sections through successive stages in development of the "nucleus" of the *Sacculina interna*. *am*, outer layer of mantle; *im*, inner layer of mantle; *m*, mesoderm cells; *o*, aperture of invagination of perisomatic cavity, not shown in B; *ov*, rudiment of ovary; *p*, perisomatic cavity. (After Delage, from Korschelt and Heider's *Embryology*.) According to G. Smith, the mantle-cavity is already established when the invagination to form the perisomatic cavity takes place as in A.

the fixed antennule, and when fully formed it becomes evaginated and forces its way through the cuticle of the host (Fig. 82, F). Through it the contents of the sac, consisting of a mass of undifferentiated cells surrounded by an ectodermal layer, pass into the body-cavity (haemocoel) of the crab, and become what Delage called the *Sacculina interna*. Probably the mass of cells is at first carried passively by the blood-currents of the host, but it ultimately becomes attached to the lower surface of the intestine

immediately behind the stomach. It now begins to send out processes which branch to form the absorptive roots, while the main part of the embryo grows backwards along the intestine towards the point at which emergence of the adult *Sacculina* takes place. A thickening near the growing border forms

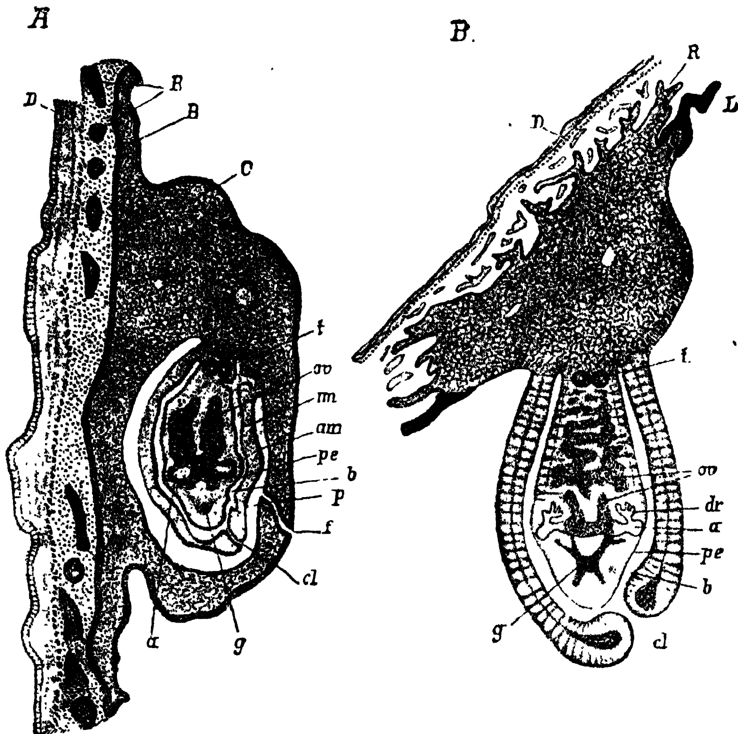


FIG. 84.

Later stages in the development of *Sacculina*. A, *Sacculina interna* fully formed. B, *Sacculina externa* just after emergence from the body of the host. *a*, genital atrium; *om*, outer layer of mantle; *B*, basal plate; *b*, mantle-cavity; *C*, central tumour; *cl*, opening of mantle-cavity; *D*, intestinal wall of host; *dr*, colleteric gland; *f*, opening of perisomatic cavity; *g*, nerve-ganglion; *im*, inner layer of mantle; *L*, integument of host; *ov*, ovary; *p*, perisomatic cavity; *pe*, ectoderm of visceral mass; *R*, root-processes; *t*, testis. (After Delage, from Korschelt and Heider's *Embryology*.)

the first rudiment of the organs of the adult, and is known as the "nucleus" (Fig. 83). Within this the mantle-cavity arises by delamination, and an outer cavity concentric with it, the "perisomatic" cavity (*p*), is formed (according to G. Smith) by an invagination of ectoderm. When the young *Sacculina* is completely formed (Fig. 84, A) it has been carried by its backward growth into the abdomen of the host, where it lies very close to the ventral

integument. Its presence causes a degeneration of the muscular and hypodermic tissues between it and the external cuticle, and at the next moult of the crab a hole is left through which the body of the parasite, protruding from the perisomatic sac, emerges on the surface (Fig. 84, B). The mantle-opening is at first closed by a plug of chitin, but in other respects the young *Sacculina externa* has already the essential structure of the adult.

The development of *Peltogaster* seems to follow much the same course as that of *Sacculina*, except that no perisomatic cavity is formed. In this genus also the parasite penetrates the cuticle and reaches the exterior without any moult of the host. Very little is known of the development in other genera of Rhizocephala. In the genus *Thompsonia* the larvae are stated to reach the *Cypris*-stage while still within the mantle-cavity of the parent.

Appendix to Rhizocephala.

The genus *Sphaerothylacus*, described by Sluiter, is parasitic on a simple Ascidian (*Polycarpa*), living attached by ramifying roots to the inner wall of the branchial sac. The globular body is enclosed in a mantle which has a small opening. There are no appendages, but there is a complete alimentary canal with mouth and anus, the latter near the mantle-opening. The two ovaries each consist of two long caeca which unite to open, with those of the opposite side, into a common atrium near the mouth, surrounded by a mass of glandular tissue, no doubt representing the colleteric glands. The testes are paired simple tubes, opening close to the anus. The nauplius larvae differ from those of the true Rhizocephala in the absence of fronto-lateral horns.

The genus *Sarcotaces*, Olsson, comprises two species which live embedded in the muscles of fish. Their structure is very imperfectly known, but an alimentary canal is said to be present and there are no "roots." The nauplius larva is without fronto-lateral horns.

The systematic position of both genera is quite obscure, and only further investigation can determine what relation, if any, they bear to the true Rhizocephala.

Remarks on Habits, etc., of Cirripedia.

The Cirripedia are exclusively marine, only a very few species penetrating into brackish water. In correlation with their sedentary habits the non-parasitic Cirripedia have developed a peculiar method of feeding by sweeping the water for floating particles of nutriment, with a net formed by the tendril-like branches of the thoracic limbs. Most species

are attached to rocks, seaweeds, etc., at the bottom, but the species of *Lepas* and other genera are found on floating timber and ships' bottoms, while in *L. fascicularis*, the colonies of which gather round small floating objects such as dead *Velellae* or *Spirula* shells, additional buoyancy is gained by a vesicular mass of secretion from the cement-glands. Many Operculata are found attached to or embedded in corals, while the pedunculate *Lithotrya* and the Acrothoracica burrow into corals and the shells of Mollusca. Various species of Pedunculata and Operculata are constantly found attached to large marine animals such as whales, turtles, and sea-snakes, or to the limbs and gills of large Decapod Crustacea. In the case of the operculate *Tubicinella*, found on whales, the shell becomes deeply embedded in the epidermis of the host. The line dividing commensalism from parasitism is definitely crossed by the pedunculate *Anelasma*, in which the mouth-parts and limbs are reduced, and the peduncle, embedded in the flesh of a shark, absorbs nourishment by ramified "roots." From this it is but a step to the parasitic and degenerate Rhizocephala, of which the habits have already been indicated.

The smallest Cirripedia are found among the Acrothoracica, some species of which are only two or three millimetres in length. Most of the Thoracica are much larger, the bulkiest being *Balanus psittacus*, of which the shell is stated to reach nine inches in height by two or three inches in diameter. The peduncle of *Lepas anatifera* may grow to 16 or 18 inches long.

PALAEONTOLOGY.

The characters and phylogenetic importance of some of the Palaeozoic Cirripedia have already been alluded to. It may be added that, like *Pollicipes*, the still existing genus *Scalpellum* dates back to the Silurian, and that both are well represented in the later Secondary rocks. Of the extinct genera, the Palaeozoic *Turrilepas* and the Cretaceous *Loricula*, already mentioned, are the most important. The earliest undoubted Operculate is *Verruca* (Asymmetrica) from the Upper Cretaceous. Many of the existing genera of Pedunculata and Operculata are found fossil in Tertiary deposits.

AFFINITIES AND CLASSIFICATION.

The great structural differences separating the Cirripedia from the other Crustacea show that they must have diverged very early from the main line of Crustacean descent. The simple biramous form of the trunk-limbs and their number have been regarded as indicating an affinity with the Copepoda, but there is little else to

support this view. The resemblance of the bivalved shell of the *Cypris* larva to that of an Ostracod extends to such characters as the asymmetry of the valves and the presence of fronto-lateral glands near the margins of the shell; but the rest of the organisation differs widely from that of the Ostracoda. Among the characters which are probably significant of the isolated position of the Cirripedia are the difference in position of the genital apertures in the two sexes and the fact that the female openings are placed farther forward than in any other Crustacea. The nature of the larval development, especially the sudden transition between the sharply contrasted nauplius and *Cypris* stages, indicates a high degree of specialisation, and the structure of the adult animals is in many respects so clearly correlated with the sessile habit and the mode of obtaining food as to afford little help in deciphering their phylogeny. It may be noted here that, like other groups of sedentary organisms, the Cirripedia show a tendency to the assumption of a superficial radial symmetry, which becomes very marked in the Operculata.

The Cirripedia were divided by Darwin into three orders, Thoracica, Abdominalia, and Apoda. The order Abdominalia contained the single genus *Cryptophialus*, which Darwin, misled by a superficial segmentation of the body, supposed to possess appendages on the abdominal region. It has been shown, however, that the appendages in question are really thoracic, and that *Cryptophialus* does not differ in this respect from *Alcippe*, which Darwin (although recognising the resemblance between the two genera) placed among the Thoracica. In the classification of Gruvel, adopted here, these two genera and some allied forms are grouped together as Acrothoracica, but it is to be noted that the differences separating this order from the Thoracica are probably less important than those distinguishing the other orders, and that the recently described *Kolcolepas* of Stebbing helps to unite the two.

The genus *Proteolepas*, the sole representative of the order Apoda, is still known only from Darwin's description of a single specimen and its affinities are obscure. In the absence of a mantle it differs widely from all other Cirripedia.

The Rhizocephala are plainly characterised as Cirripedia by their larval stages, but much remains to be done in elucidating the relationships of some of the genera at present referred provisionally to this order. The Ascothoracica form another order, established since the date of Darwin's work, but many points in their morphology and development are still too imperfectly known to allow of their systematic relations being precisely defined.

SUB-CLASS CIRRIPEDIA.

ORDER 1. **Thoracica.**

A mantle present. Six pairs of cirriform trunk-appendages.

SUB-ORDER 1. **Pedunculata.**

Peduncle and capitulum distinct. Outer plates of shell, when present, not forming a "wall."

Family LEPADIDAE. *Lepas*, Linn. (Fig. 57, A); *Dichelaspis*, Darwin; *Pollicipes*, Leach (Fig. 60); *Scalpellum*, Leach (Fig. 61); *Ibla*, Leach (Fig. 71); *Lithotrya*, Sowerby; *Conchoderma*, Olfers; *Alepas*, Rang; *Anelasma*, Darwin (Fig. 68); *Koleolepas*, Stebbing.

SUB-ORDER 2. **Operculata.**

No peduncle. Scuta and terga forming a movable operculum. Outer plates of shell coalesced to form a "wall."

TRIBE 1. ASYMMETRICA.

Scutum and tergum of one side movable, without depressor muscles.

Family VERRUCIDAE. *Verruca*, Schum.

TRIBE 2. SYMMETRICA.

Scuta and terga of both sides movable, with depressor muscles.

Family BALANIDAE. *Balanus*, Lister (Fig. 57, B); *Coronula*, Lamarck; *Tubicinella*, Lamarck; *Xenobalanus*, Steenstrup (Fig. 65); *Elminius*, Leach; *Pyrogoma*, Leach. Family CHTHAMALIDAE. *Chthamalus*, Ranzani; *Catophragmus*, Sowerby (Fig. 62); *Octomeris*, Sowerby.

ORDER 2. **Acrothoracica.**

A mantle present. Trunk-appendages reduced in number, the posterior pairs widely separated from the first pair.

Family ALCIPPIDAE. *Alcippe*, Hancock (*Trypetesa*, Norman) (Fig. 72). Family KOCHLORINIDAE. *Kochlorine*, Noll. Family CRYPTOPHIALIDAE. *Cryptophialus*, Darwin.

ORDER 3. **Ascothoracica.**

Mantle containing diverticula of alimentary canal. Trunk-appendages more or less reduced.

Family LAURIDAE. *Laura*, Lacaze-Duthiers (Fig. 76). Family SYNAGOGIDAE. *Synagoga*, Norman. Family PETRARCIDAE. *Petrarca*, Fowler. Family DENDROGASTRIDAE. *Dendrogaster*, Knipowitsch (Fig. 78).

ORDER 4. **Apoda.**

Mantle absent. No trunk-appendages.

Family PROTEOLEPADIDAE. *Proteolepas*, Darwin (Fig. 79).

ORDER 5. Rhizocephala.

Mantle present. No appendages nor alimentary canal. A system of absorptive roots nearly always present.

Families not defined. Probably several should be recognised. *Peltogaster*, Rathke; *Sacculina*, Thompson (Fig. 80); *Sylon*, Kroyer; *Clistosaccus*, Lilljeborg; *Lernaeodiscus*, F. Muller; *Triangulus*, Smith; *Duplorbis*, Smith; *Thompsonia*, Kossmann.

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CHAPTER VI

THE MALACOSTRACA

SUB-CLASS MALACOSTRACA, Latreille (1806).

SERIES I. LEPTOSTRACA.

DIVISION PHYLLOCARIDA.

Order **Nebaliacea.**

SERIES II. EUMALACOSTRACA.

DIVISION 1. SYNCARIDA.

Order **Anaspidacea.**

DIVISION 2. PERACARIDA.

Order 1. **Mysidacea.**
„ 2. **Cumacea.**
„ 3. **Tanaidacea.**
„ 4. **Isopoda.**
„ 5. **Amphipoda.**

DIVISION 3. EUCARIDA.

Order 1. **Euphausiacea.**
„ 2. **Decapoda.**

DIVISION 4. HOPLOCARIDA.

Order **Stomatopoda.**

Definition.—Crustacea in which the carapace is variously developed or may be vestigial; there are typically fourteen (rarely fifteen) trunk-somites, all of which (except the fifteenth) bear appendages; the telson rarely has a caudal furca; antennules often biramous; the mandibles may have a palp; the trunk-limbs are differentiated into two tagmata, a thoracic of eight and an abdominal of six pairs; female genital apertures on the sixth,

male apertures on the eighth trunk-somite; paired eyes usually present; development usually with metamorphosis, young rarely hatched in nauplius stage.

The sub-class Malacostraca includes such a diversity of forms that it will be necessary to deal more fully than in the case of the other sub-classes with the separate orders composing it. Before doing so a brief account must be given of the general type of organisation found throughout the sub-class.

Apart from the fixed number of somites, to which the Leptostraca offer the only exception, the most characteristic feature of the Malacostraca is the separation of the trunk-limbs into sharply defined thoracic and abdominal tagmata. This, together with the constancy in position of the genital apertures, on different somites in the two sexes, is sufficient to demonstrate the unity of the sub-class.

Leaving the Leptostraca aside for the present, the more primitive members of each of the "divisions" in the scheme of classification here adopted approximate to a common type of structure from which the more specialised members of each group diverge very widely. Thus, the possession of a carapace enveloping the thoracic region, movably stalked eyes, biramous antennules, a scale-like exopodite on the antenna, natatory exopodites on the thoracic limbs, an elongated and ventrally flexed abdomen, and a "tail-fan" formed by the lamellar rami of the last pair of appendages spread out on either side of the telson, are characters common to the Mysidacea, Euphausiacea, and the lower Decapoda, and, with some modifications, to the Anaspidacea and Stomatopoda. It seems reasonable to suppose that this combination of characters, making up what has been called the "caridoid facies," must be attributed to the hypothetical common stock of the Malacostraca. At all events, it is possible to represent, in diagrammatic fashion, a generalised Malacostracan which serves as a convenient summary of the morphology of the group (Fig. 85). Some of the characters of this type require to be considered in more detail.

The *antennule*, as already stated, is biramous, having two flagella springing from a peduncle of three segments. Since the antennules in the other sub-classes are always uniramous, as they are in the nauplius, it seems probable that the two flagella do not represent the endopodite and exopodite. When only one flagellum is present in the Malacostraca it is the outer which persists, and it alone, as is shown by the sensory filaments which it carries, corresponds to the single ramus of the other sub-classes. In certain Decapoda (Caridea) and in Stomatopoda there are three flagella, the outer flagellum being divided into two.

The protopodite of the *antenna* is composed of two or of three

segments. According to Hansen the latter number is, here as elsewhere, the more primitive. The endopodite is flagelliform, and the expodite has the form of a plate, the so-called "scale" or "squama," probably of use in swimming. As a rule the first three segments of the endopodite are enlarged and are counted with the two (or three) segments of the protopodite as forming a five- (or six-) segmented *peduncle*.

The *mandible* has a "palp" of three segments, never biramous. The oral edge of the mandible is more or less distinctly divided into a "molar process" and an "incisor process," and between them is armed with bristles or spines. An accessory blade, the *lacinia mobilis*, lying close to the cutting edge of the incisor process and apparently

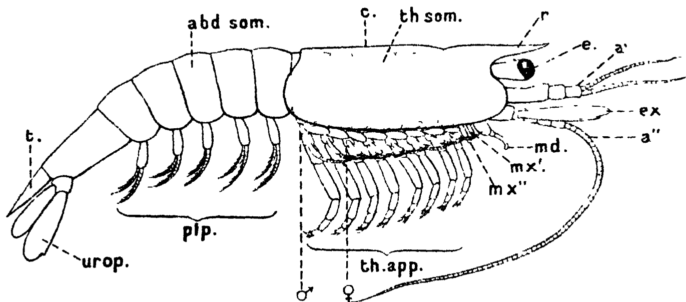


FIG. 85.

Diagram of a generalised type of Malacostraca showing the "caridoid facies." *a'*, antennule; *a"*, antenna; *abd.som*, abdominal somites; *c*, carapace; *e*, eye; *ex*, exopodite of antenna; *md*, mandible; *mx'*, maxillula; *mx"*, maxilla; *plp*, pleopods; *r*, rostrum; *t*, telson; *th.app*, thoracic appendages; *urop*, uropods; ♂ and ♀ indicate the positions of the genital apertures in the male and female sex respectively.

formed by the enlargement of one of these spines, is found in some of the orders, and is perhaps also a primitive character.

The *maxillulae* have two endites and a "palp" of several segments. According to Hansen, whose investigations on the skeletal framework of the mouth-parts will be often referred to, the two endites belong to the first and third segments of the appendage, a small sclerite which Hansen supposes to represent the second segment having no endite in connection with it. An exite, in the form of a rounded plate, may be present; according to Hansen it belongs to the first segment. The *maxillae* are more complex in form and the primitive plan of their structure is not quite clear. Apparently there are two endites, each of which is bifid, corresponding to the second and third segments, and a palp of one or two segments.

The *thoracic appendages* (Fig. 86) are all similar, none of them, in the primitive type, being differentiated as maxillipeds. Each has a protopodite of two segments, the coxopodite and basipodite, with,

according to Hansen, a pre-coxal segment (pleuropodite of Coutière) which is distinct only in the Leptostraca and Stomatopoda. The axis of the limb is continued by the endopodite which forms an ambulatory leg, while the flagelliform exopodite is used for swimming. There are five segments in the endopodite, termed by Milne-Edwards respectively the ischiopodite, meropodite, carpopodite, propodite, and dactylopodite (often abbreviated to ischium, merus, carpus, propodus, and dactylus). Hansen considers that the terminal claw which is sometimes distinct from the dactylopodite represents an additional segment, making, with the pre-coxa, nine segments in the axis of the limb instead of the seven usually recognised. It seems probable, however, that this claw (termed stylopodite by Coutière) is simply an enlarged spine and not one of the segments of the limb.

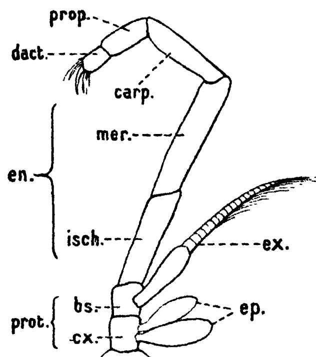


Fig. 86.

Diagram of a Malacostracan thoracic appendage. *bs*, basipodite; *carp*, carpopodite; *cx*, coxopodite; *dact*, dactylopodite; *en*, endopodite; *ep*, epipodites; *ex*, exopodite; *isch*, ischiopodite; *mer*, meropodite; *prop*, propodite; *prot*, protopodite.

At the bases of the thoracic limbs on the outer side are a series of epipodial appendages (exites) probably originally branchial in function. It is not quite clear how many of these appendages must be attributed to each thoracic limb of the primitive type, but probably at least two are to be recognised, an *epipodite* attached to the coxopodite and a *proepipodite* to the pre-coxal segment. The *oostegites*, or brood-plates, attached to the inner side of the coxopodite in the female sex in some of the orders, and forming a pouch for the protection of the eggs and young, may possibly be derived from some of these epipodial structures, as Claus suggests. The terminology applied to the thoracic limbs in systematic works differs greatly in the various orders of Malacostraca. From one to three of the anterior pairs may be called *maxillipeds*, the second and third pairs are in some cases known as *gnathopods*, and the last five pairs are often termed *peraeopods.*

The abdominal appendages are all biramous and are used in swimming, but the sixth pair differ in form and function from the others. The first five pairs are known as *pleopods.* They have the protopodite composed of two segments (occasionally there are traces of a third), and the rami are fringed with long setae and assist the thoracic exopodites in the ordinary swimming movements of the animal. The appendages of each pair are coupled together by a group of hooked spines (retinacula) either on the inner edge of the protopodite or on a special process of the

endopodite known as the *appendix interna*. The sixth pair of abdominal appendages, known as the *uropods*, are larger than the others, with a short, unsegmented protopodite and broad lamellar rami which lie at the sides of the telson and form with it the "tail-fan" which is used in swimming, or rather springing, backwards by sudden flexion of the whole abdomen.

The Leptostraca alone among the more primitive orders of existing Malacostraca stand apart from the scheme outlined above, and seem to have diverged from the main line of Malacostracan descent before the assumption of the caridoid form. Their systematic relations will be discussed more fully later.

Classification of the Malacostraca.

The group Malacostraca, established by Latreille in 1806, has been accepted as a natural division by nearly all subsequent writers. Almost the only divergences of opinion as to its limits have had reference to the Leptostraca, which many zoologists following Milne-Edwards have referred to the Branchiopoda or have regarded as occupying an intermediate place between Malacostraca and "Entomostraca." Claus's investigations on the structure of *Nebalia*, however, have been generally accepted as demonstrating its Malacostracan affinities. In the arrangement here adopted (following Grobben) the order Nebaliacea is included within the sub-class Malacostraca, but its distinctness from the other orders is marked by placing it in a separate division (Leptostraca) opposed to the other orders grouped together as Eumalacostraca.

In the arrangement of the Eumalacostraca most carcinologists hitherto have followed the lines laid down by Leach, who, in 1815, divided the group into two legions—the Podophthalma and the Edriophthalma—according to the condition of the eyes, movably pedunculate in the one and sessile in the other. As originally defined, the two groups were also distinguished from each other by the presence in the Podophthalma of a carapace which was absent in the Edriophthalma, this character giving occasion for the names Thoracostraca and Arthrostraca applied to the same groups by Burmeister in 1834. The progress of research, however, rendered it increasingly difficult to frame satisfactory definitions of the two divisions. Thus, the sessile-eyed Tanaidacea were found to possess a true, though reduced, carapace, while the Cumacea were still more plainly intermediate between the two groups. The recent discovery of the very remarkable genus *Anaspides*, which has stalked eyes but no carapace, and the closely allied *Koonunga* with sessile eyes, makes the retention of the old arrangement quite impossible.

An important departure from the line of classification generally followed was made in 1883 by Boas, who showed that the order "Schizopoda" as then understood comprised two very different groups, which he separated as distinct orders, the Euphausiacea and Mysidacea. Boas discarded the old divisions Podophthalma and Edriophthalma, and divided the Malacostraca into seven orders, Euphausiacea, Mysidacea, Cumacea, Isopoda, Amphipoda, Decapoda, and Squillacea (or Stomatopoda). Hansen, in 1893, carried the reform of the classification a step further. Setting apart (as Huxley had previously done) the aberrant Stomatopoda, as well as the Leptostraca, he showed that the remaining Malacostraca fell into two well-defined groups, the line of division passing through the old order Schizopoda; on the one side he placed the Euphausiacea with the Decapoda, and on the other the Mysidacea with the Cumacea and the Edriophthalmate orders Tanaidacea, Isopoda, and Amphipoda. The classification adopted here is essentially that of Hansen, as modified and extended by the present writer in 1904.

It will be convenient to give here definitions of the main groups into which the Malacostraca are divided. The orders will be considered in greater detail in the subsequent chapters.

Sub-Class Malacostraca.

Series I. **Leptostraca**, Claus (1880).

Abdomen of seven somites, the last of which is without appendages, and a telson bearing a pair of movably articulated furcal rami; an adductor muscle runs between the two valves of the carapace; thoracic limbs all similar, more or less foliaceous, with protopodite of three segments.

Series II. **Eumalacostraca**, Grobben (1892).

Abdomen of six somites (the number may be reduced by coalescence), the last of which typically bears a pair of appendages, and a telson which never bears movable furcal rami; no adductor muscle of the carapace; thoracic limbs rarely all similar (Euphausiacea), typically pediform, protopodite of two segments except in Stomatopoda.

Division 1. Syncarida, Packard (1886).

Carapace absent; first thoracic somite fused with the head or defined therefrom by a groove; protopodite of antenna of two segments; mandible without lacinia mobilis; thoracic legs flexed between fifth and sixth segments; no oostegites; no appendix interna on pleopods; hepatic caeca numerous; heart much elongated, tubular.

DIVISION 2. PERACARIDA, Calman (1904).

Carapace, when present, leaving at least four of the thoracic somites distinct; first thoracic somite always fused with the head; protopodite of antenna typically of three segments; mandible with lacinia mobilis (except in parasitic and other modified forms); thoracic legs flexed between fifth and sixth segments; oostegites attached to some or all of the thoracic limbs in female, forming a brood-pouch; no appendix interna on pleopods; hepatic caeca few and simple; heart generally elongated, extending through the greater part of thoracic region, or displaced into abdomen; spermatozoa generally filiform; development taking place within the brood-pouch, young set free at a late stage.

DIVISION 3. EUCARIDA, Calman (1904).

Carapace coalescing dorsally with all the thoracic somites; eyes pedunculate; protopodite of antenna with, at most, two distinct segments; mandible without lacinia mobilis in adult; thoracic legs flexed between fourth and fifth segments; no oostegites; an appendix interna sometimes present on pleopods; hepatic caeca much ramified; heart abbreviated, thoracic; spermatozoa spherical or vesicular, often with radiating appendages; development as a rule with metamorphosis, a free-swimming nauplius stage in the more primitive forms.

DIVISION 4. HOPLOCARIDA, Calman (1904).

Carapace leaving at least four of the thoracic somites distinct; two movable segments are separated from the anterior part of the head, bearing respectively the pedunculate eyes and the antennules; protopodite of antenna of two segments; mandible without lacinia mobilis; posterior thoracic limbs with protopodite of three segments (the relation of the segments of the anterior thoracic limbs to those of the limbs in the other divisions is doubtful); an appendix interna on pleopods; hepatic caeca much ramified; heart much elongated, extending through thoracic and abdominal regions; spermatozoa spherical; development with metamorphosis, a free-swimming nauplius stage is not certainly known.

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CHAPTER VII

THE LEPTOSTRACA

SERIES LEPTOSTRACA, Claus (1880).

DIVISION PHYLLOCARIDA, Packard (1879).

Order **Nebaliacea.**

Definition.—To the characters mentioned on p. 148 as distinctive of the series the following may be added: Carapace present; all the thoracic somites distinct; eyes pedunculate; mandible without lacinia mobilis; no oostegites; first four pairs of abdominal appendages biramous, with appendix interna, last two pairs reduced; hepatic caeca few; heart elongated; development embryonic, young set free at a late stage.

Historical.—The first-known member of the Leptostraca was the *Cancer bipes* of O. Fabricius, described from Greenland. Leach, who in 1815 established the genus *Nebalia*, placed it among the Macrura, but H. Milne-Edwards, while admitting its affinities with *Mysis*, ranked it as a Phyllopod, and this view was long and widely held. Metschnikoff in 1865, from a study of its development, replaced the genus among the Malacostraca as a "phyllopodiform decapod." Claus, in a series of memoirs ending with his exhaustive monograph of 1889, vindicated the title of *Nebalia* to rank as a Malacostracan, and placed it in a group Leptostraca, alongside the Arthrostraca and Thoracostraca. The resemblance of certain fossil Crustacea to *Nebalia* had long been recognised, and Packard in 1879 proposed the name Phyllocarida for the group, including the living and fossil genera. Sars has called attention to the similarity in general form between *Nebalia* and certain Copepoda, but Claus showed this resemblance to be merely superficial.

MORPHOLOGY.

The carapace (Fig. 87) is compressed laterally so as to form a bivalved shell (though without any definite hinge-line), loosely enveloping the thorax and more or less of the abdomen, and quite

concealing, in most cases, the thoracic limbs. The two halves of the shell can be approximated by the action of an adductor muscle traversing the body in the region of the maxillae. Anteriorly, the carapace is produced into a movably articulated rostral plate (*r*), not provided with special muscles but elevated or depressed by the movements of the underlying parts. The carapace is not attached to the body behind the maxillary region, and the eight thoracic somites which, except in *Nebaliopsis*, are very short and crowded together, are all distinctly marked off by grooves on the delicate integument. Of the abdominal somites the fourth alone may have distinct pleural plates, or these may be altogether absent. The telson (*t*) bears the two styliform or lamellar furcal rami (*f*)

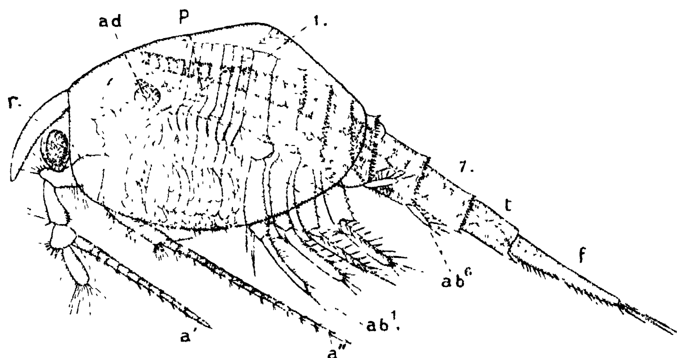


Fig. 87.

Nebalia bipes, ♀, from the side. *a'*, antennule; *a''*, antenna; *ab*1, *ab*6, first and sixth abdominal appendages; *ad*, adductor muscle of carapace; *f*, caudal furca; *p*, palp of maxillula; *r*, rostral plate; *t*, telson; 1, 7, first and seventh abdominal somites. (After Claus.)

articulated with it and moved by special muscles; the anus opens between the rami towards the ventral side.

Appendages.—The *antennules* (Fig. 88, A) have a peduncle of four segments bearing a flagellum of varying length and, external to it, a movable scale. It seems probable that this scale represents the outer ramus of the antennule of other Malacostraca, and the occurrence of four (instead of three) segments in the peduncle is paralleled in certain species of Tanaidacea.

The peduncle of the *antenna* (Fig. 87, *a''*) is apparently composed of four segments, of which the last two are coalesced in *Nebalia* and *Paranebalia*. Hansen recognises, in addition, a short basal segment and another, very short, between the second and third of the larger segments. The exopodite is absent. The distal part of the endopodite forms a flagellum which, in the adult male, may be nearly as long as the body.

The *mandible* (Fig. 88, B) has a strong molar process; the

incisor process is small and simple in *Nebalia* and *Paranebalia*, large and toothed in *Nebaliella*, and absent in *Nebaliopsis*. The palp is large and has three segments.

The *maxillula* (Fig. 88, C) has the usual two endites. The palp is vestigial in *Nebaliopsis*; in the other genera it is attached to the distal margin but curves outwards and backwards so that the

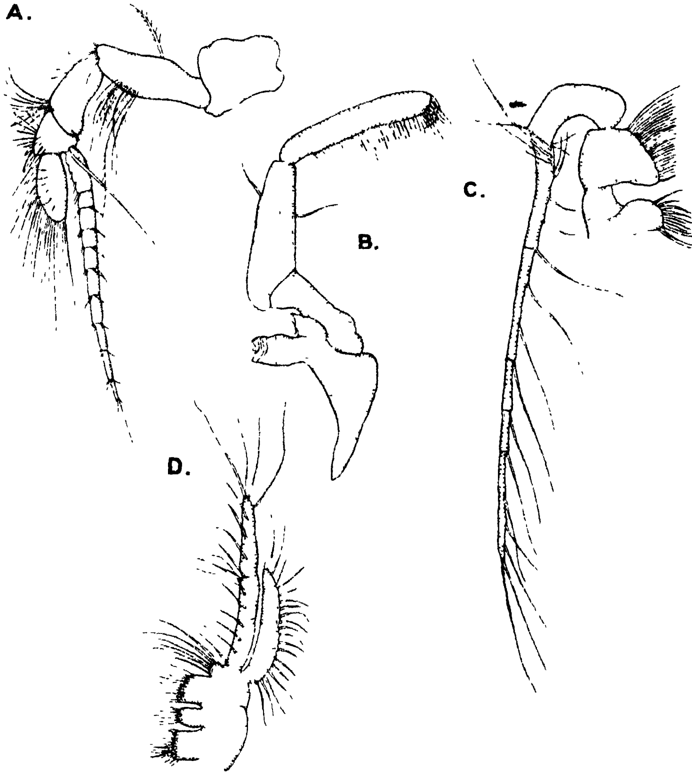


FIG. 88.
Cephalic appendages of *Nebalia*. A, antennule; B, mandible; C, maxillula; D, maxilla. (After Claus.)

very long, slender, and indistinctly segmented flagellum in which it terminates is directed obliquely upwards along the side of the thorax underneath the carapace (Fig. 87, *p*).

The *maxillae* (Fig. 88, D) approximate in general form to the thoracic limbs, except for the absence of an epipodite. There are generally four endites, but the distal one is much reduced in *Nebalia* and *Paranebalia*. The endopodite is divided into two segments in *Nebalia* and, like the exopodite, is generally elongated.

In *Nebaliopsis,* however, the endopodite is a short lobe and the exopodite is hardly indicated.

The eight pairs of *thoracic limbs* are all similar, except in *Nebaliopsis,* and they present considerable differences of structure in the four genera.

In *Nebalia* (Fig. 89) the whole limb is much flattened. The broad coxopodite and basipodite are distinctly separated, and on the proximal side of the former Hansen has detected a small pre-coxal segment. To the outer margin of the coxopodite is attached the broad lamellar epipodite (*ep*), obscurely divided into

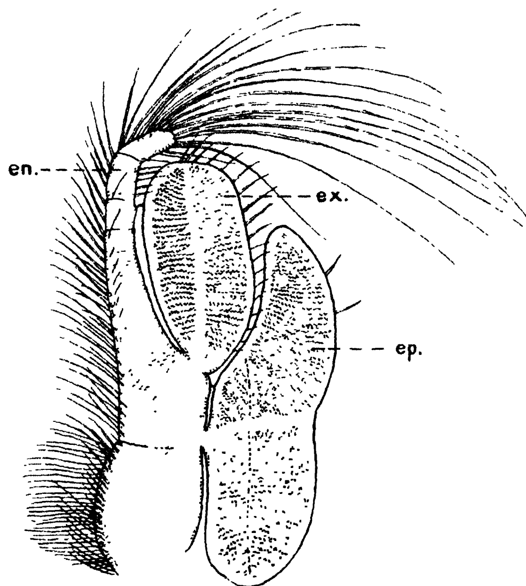


FIG. 89.
First thoracic limb of *Nebalia*. *en*, endopodite ; *ep*, epipodite ; *ex*, exopodite. (After Claus.)

a proximal and a distal lobe by a slight notch on the outer margin opposite the point of attachment. The basipodite bears externally the oval flattened exopodite (*ex*) and is continued without any distinct line of articulation into the narrower endopodite (*en*). From the distal end of the endopodite three, or, in the case of the eighth pair, four segments are marked off, so that, except for the absence of an articulation between the basipodite and ischiopodite, all the segments of the typical malacostracan leg can be distinguished. In *Nebaliella* (Fig. 90, B) the epipodite is absent, the exopodite has more numerous marginal setae, and the articulation between the basipodite and ischiopodite is more distinctly

marked. In *Paranebalia* (Fig. 90, A) the endopodite is long and slender, projecting beyond the edges of the carapace in the natural

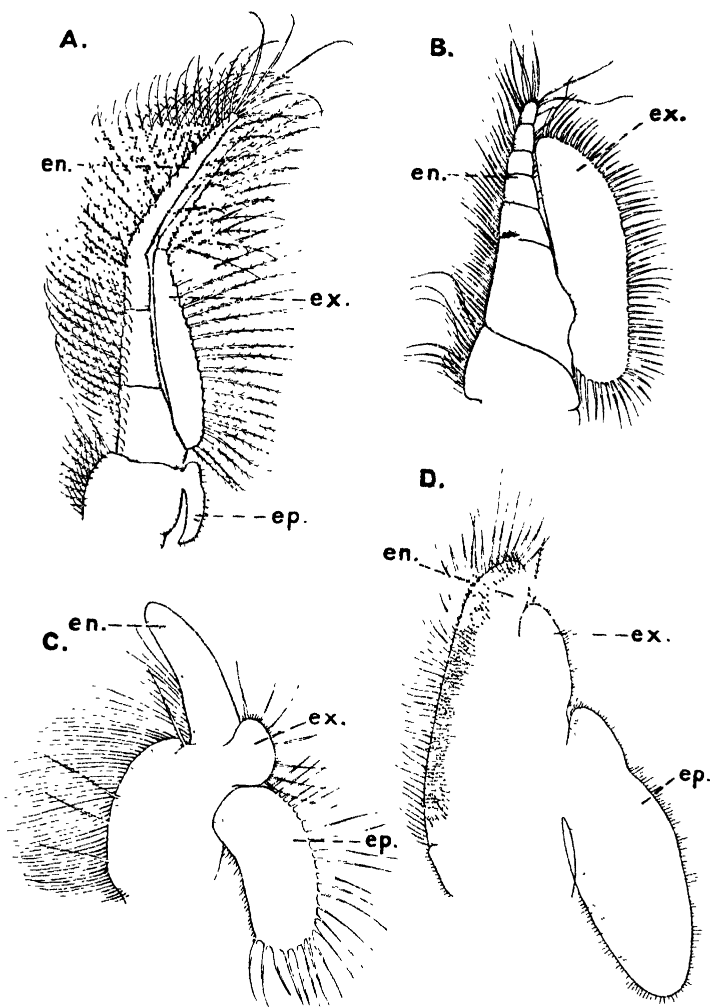


FIG. 90.

Thoracic limbs of Leptostraca. A, *Paranebalia longipes*, fifth limb. B, *Nebaliella antarctica*, fourth limb. C, *Nebaliopsis typica*, first limb. D, the same, second limb. *en*, endopodite ; *ep*, epipodite ; *ex*, exopodite. (A after Sars ; B, C, D after Thiele.)

position. The exopodite is also long and narrow, and is provided, on its outer edge, with numerous long plumose setae which suggest a natatory function. The epipodite is very small. The ischio-

podite is defined from the basipodite, at least in the last pair, and Hansen recognises a minute terminal segment as well as a pre-coxal, making altogether nine segments in the axis of the limb. In *Nebaliopsis* the thoracic limbs are very different from those of the other genera. Except the first and last pairs, they are unsegmented lanceolate lamellae (Fig. 90, D), having a slight lobe on the outer edge to represent the exopodite, and a more distinctly marked bilobed epipodite; the inner edge is beset with setae along its whole length. In the last pair, which are almost without setae, a terminal segment is marked off, and in the first pair (Fig. 90, C) this part, although not distinctly segmented off, is produced into a finger-shaped distal lobe (*en*).

In *Nebalia* the tip of each of the thoracic limbs carries, in the breeding female, a fan of long plumose setae turned inwards to form the floor of a basket-like brood-chamber which is closed behind by rows of long setae on the inner edges of the last pair.

The first four pairs of abdominal appendages are biramous and are used in swimming; the last two pairs are small and uniramous. The former (Fig. 91) have a stout protopodite of two segments and long indistinctly segmented rami fringed with spines and plumose setae. From the inner edge of the endopodite close to its base there springs a short *appendix interna* (*a.i*) bearing a group of hooked spines at its tip.

Alimentary System.—The masticatory stomach, in *Nebalia*, is of a comparatively simple type. It is divided into a "cardiac" and a "pyloric" portion, the former with masticatory ridges moved by muscles, and the latter with two pairs of lateral setose lobes and a dorsal groove which is continued as a delicate chitinous funnel, open below, some distance into the mid-gut. The mid-gut extends back to the penultimate segment of the body. Four pairs of hepatic caeca open near its anterior end and a pair of short caeca open separately on the ventral side in the same region. Near its junction with the proctodaeum the mid-gut gives off an unpaired dorsal caecum, bifid at the tip.

Circulatory System.—The *heart*, in *Nebalia*, extends from the cephalic region to the fourth abdominal somite. It has seven pairs of ostia, and the last pair, which are larger than the others, are situated in the region of the sixth thoracic somite. The exopodites and epipodites of the thoracic limbs are traversed by a close network of blood-channels and no doubt serve as respiratory organs. The valves of the carapace probably also assist in respiration, and the blood circulating in them is returned to the pericardial sinus by a definite venous channel on each side.

Excretory System.—Both the *antennal* and the *maxillary glands* are present in a vestigial condition, the former lying in the proximal segment of the antennal peduncle, while the latter is

placed close to the adductor muscle of the carapace at the base of the maxilla. The gland in each case consists of a minute saccule giving off a short duct, but the external openings have not been detected.

Eight pairs of glands lying at the bases of the thoracic limbs are also believed to be excretory. Each consists of a thickening of

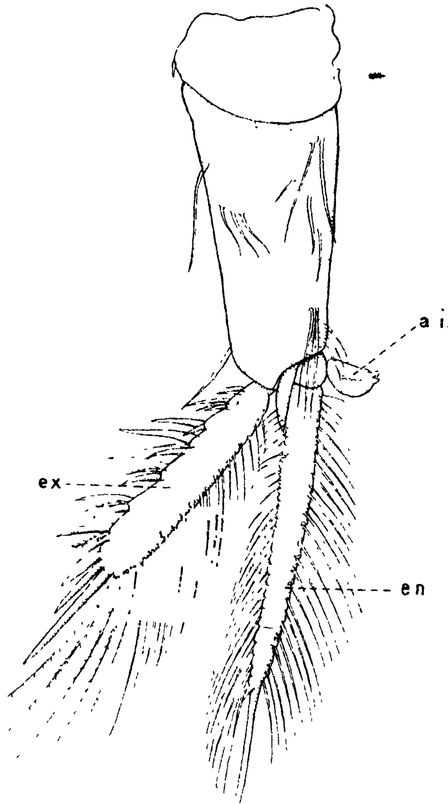


FIG. 91.
Pleopod of second pair of *Nebalia*. *a.i*, appendix interna; *en*, endopodite; *ex*, exopodite. (After Claus.)

the hypodermis partly surrounding the efferent blood-channel from the epipodite. These glands alone become coloured by *intra vitam* treatment with indigo-carmine, while the antennal and maxillary glands excrete particles of carmine when the animal has been fed with that substance.

Muscular System.—The *adductor muscle* (Fig. 87, *ad*) of the carapace has two muscular heads attached to the valves and con-

nected by a median tendinous part which passes under the stomach in the region of the maxillae. The muscle is innervated from the maxillary ganglion.

Nervous System. — The brain is complex, admitting of close comparison with that of other Malacostraca. The oesophageal connectives are short and are united by the commissure of the antennal ganglia behind the oesophagus. In the ventral chain the ganglia of the mandibular, maxillular, and maxillary somites are distinct, though, like the eight thoracic ganglia, they are closely crowded together. Six abdominal ganglia are present, the seventh somite, like the telson, having no ganglion in the adult. In the embryo, however, a transitory seventh abdominal ganglion has been found.

Sense-Organs.—The eyes are stated to resemble, in their intimate structure, those of the Mysidacea. In *Nebaliella* and *Nebaliopsis* and in one species of *Nebalia* (*N. typhlops*) the eyes are vestigial, though the peduncles persist. On the upper and inner surfaces of the ocular peduncle, in *Nebalia*, there are two small tubercles, supposed to be sensory organs. Olfactory filaments of the usual type are present on the antennules and, in the male, also on the antennae.

Reproductive System.—The most conspicuous external difference between the sexes consists in the much greater length of the antennal flagellum in the male. The *gonads* have the form of paired tubes extending, when mature, through nearly the whole length of the body. The short *vasa deferentia* open on papillae on the coxopodites of the last thoracic limbs. The oviducts are hard to detect, but they appear to open on the sixth thoracic somite. The spermatozoa are spherical and are aggregated into globular spermatophores. The eggs are carried, as already stated, between the thoracic feet of the female.

Development.—The development of *Nebalia* takes place within the brood-chamber of the parent without any free-swimming larval stages, and presents many points of resemblance to that of the Mysidacea. The first three pairs of appendages appear simultaneously, giving a well-marked nauplius stage. The remaining appendages develop in order from before backwards. The embryo becomes free from the egg-membrane at a stage when all the thoracic appendages, and sometimes also those of the abdomen, are marked off (Fig. 92). The carapace at this stage does not extend beyond the second thoracic somite. When the young leave the maternal brood-chamber they have attained, in all essential respects, the structure of the adult.

Remarks on Habits, etc.

All the Leptostraca are marine. Most of the species occur in shallow water or at moderate depths, but *Nebaliopsis* belongs to the "bathypelagic" fauna at depths exceeding 1000 fathoms. Many have an extremely wide distribution, the common European *Nebalia bipes*, for instance, ranging from Greenland to Chile and Japan. The species named appears to be very resistant to unfavourable conditions, thriving in water which is foul with decaying matter. Locomotion is effected by powerful strokes of the anterior four pairs of pleopods. The thoracic limbs serve the purpose of respiration, and by their rhythmic movements produce a current of water which brings food-particles to the mouth. The water is drawn in from behind and expelled in a stream below the rostral plate.

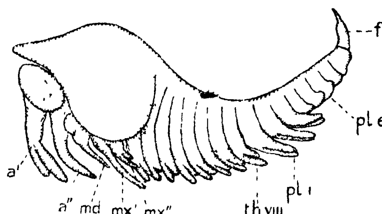


Fig. 92.

Embryo of *Nebalia*, just hatched. *a'*, antennule; *a''*, antenna; *f*, caudal furca; *md*, mandible; *mx'*, maxillula; *mx''*, maxilla; *pl.*[1], first pleopod; *pl.*[6], sixth pleopod; *th.*viii, last thoracic appendage. (After Claus.)

The largest of existing Leptostraca is *Nebaliopsis typica*, Sars, which reaches a length of about 40 mm. The other species are from 4 to 12 mm. in length.

Palaeontology.

Certain fossil Crustacea, generally grouped together as a family, Ceratiocaridae, are believed to be more or less closely allied to the existing Leptostraca. The various genera, ranging from the Cambrian to the Triassic epochs, differ considerably among themselves, but the more typical forms, such as *Ceratiocaris* (Fig. 93) and *Hymenocaris*, resemble *Nebalia* in general form, having a bivalve carapace, sometimes with an articulated rostral plate, and an extended abdomen. Nothing is definitely known of the appendages. A pair of serrated plates observed within the outline of the shell in some instances have been described as "gastric teeth," but may possibly be the mandibles (*m*). Some of the fossils are of great size, *Ceratiocaris*, from Ordovician and Silurian rocks, reaching a length of two feet.

The chief difference which can be observed between the fossils and the living representatives of the Leptostraca is that, in the former, the terminal appendages of the abdomen are always more

numerous. In most cases there are three such appendages, the telson being produced as a median style between the furcal rami.

Affinities and Classification.

The alliance of the Leptostraca with the other Malacostraca is amply justified by the agreement in the number of the appendages, by the sharp distinction between the thoracic and abdominal series, and by the position of the genital apertures. Other characters, probably of less importance, are the biramous form of the antennules, the possession of a masticatory stomach, and the complex structure of the brain. The most important differences from the Eumalacostraca are the presence of an additional somite in the abdomen, of a caudal furca, and of an adductor muscle of the carapace.

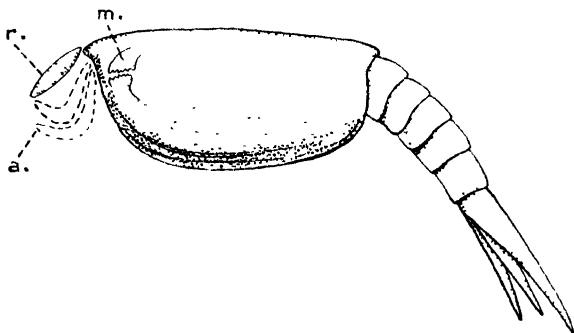


Fig. 93.
[illegible] *a*, traces of antennules (?); *m*, toothed plates, possibly the mandibles; *r*, rostal plate. (After H. Woodward.)

These are no doubt primitive features and indicate that the Leptostraca diverged from the Malacostracan stock before the assumption of the typical caridoid form. It may be suggested that the development of the uropods to form a tail-fan in the primitive Eumalacostraca was associated with the loss of the caudal furca.

The resemblance of the lamellar thoracic limbs of *Nebalia* to those of the Branchiopoda, which has led to the Leptostraca being associated in many classifications with that group, is doubtless significant, and it becomes still more striking in the case of *Nebaliopsis*. The absence of endites in the Leptostracan limb, however, is an important difference. According to the view, already mentioned (p. 42), that the exopodite is represented, in the appendages of *Apus*, for example, not by the flabellum but by the sixth endite, it would seem impossible to draw a close comparison with the appendages of *Nebalia*. Without going so far as this, however, it may be suggested as a possibility that the

"phyllopod" form of the thoracic limbs in the Leptostraca may be to some extent secondary, having arisen by suppression of the locomotor function in limbs of the more typical Malacostracan form. In this case *Paranebalia*, in which the phyllopod character of the thoracic appendages is very little marked, would be more primitive than *Nebalia* and *Nebaliopsis*.

It is difficult to decide how much importance should be given to the presence of an adductor muscle as indicating an affinity between the Leptostraca and the Conchostraca, but the possession by the former of a mandibular palp and well-developed maxillae forbid their being derived directly from any of the existing Branchiopoda.

As regards the relation of the Leptostraca to the various groups of Eumalacostraca, there seems to be a general agreement that their nearest allies are to be sought among the Mysidacea, which they resemble especially in their mode of development. It may be necessary to mention that, apart from a vague similarity in general form, perhaps the result of a similarity in habits, there is no ground for the supposition that they have any direct affinity with the Cumacea.

The four existing genera of Leptostraca may, for the present, be referred to a single family. In the absence of information as to the structure of the limbs in the fossil Ceratiocaridae, it is not possible to assign them to a definite systematic position in relation to the living forms.

ORDER **Nebaliacea**, Calman (1904).

Family NEBALIIDAE. *Nebalia*, Leach; *Paranebalia*, Claus; *Nebaliopsis*, G. O. Sars; *Nebaliella*, Thiele.

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CHAPTER VIII

THE SYNCARIDA

DIVISION SYNCARIDA, Packard (1886).

Order **Anaspidacea.**

Definition.—To the characters mentioned on p. 148 as distinctive of the Division, the following may be added: Thoracic limbs with exopodites (except the last, or the last two pairs), and with a double series of lamellar epipodites attached to the outer side of the coxopodites (except the last pair); the first pair may have gnathobasic endites on the coxopodite; pleopoda with the endopodite reduced or absent except in the first two pairs in the male sex; uropods lamellar, forming, with the telson, a tail-fan; a statocyst is present in the basal segment of the antennules.

Historical.—*Anaspides tasmaniae* was first described by G. M. Thomson in 1892, and more fully in 1894. He placed it among the "Schizopoda," establishing for it the family Anaspidae. In 1897 the present writer discussed some points in its morphology and called attention to its resemblance to certain fossil Crustacea for which Packard had established the group Syncarida. In 1904 Grobben (in his edition of Claus's *Lehrbuch der Zoologie*) referred *Anaspides* to a new subdivision of the Malacostraca which he termed Anomostraca, and in the same year the system of classification adopted here was published. Quite recently a new and very remarkable representative of the Syncarida has been discovered and described by Mr. O. A. Sayce under the name *Koonunga cursor.* It has been suggested that *Bathynella natans*, described by Vejdovsky in 1882, also belongs to this group, but our knowledge of the structure of this minute form is still very imperfect.

MORPHOLOGY.

The body, in the living Syncarida, is elongated and subcylindrical, with all the trunk-somites distinct from each other. In *Anaspides* (Fig. 94) the anterior limit of the first thoracic

somite appears to be marked by a transverse "cervical groove" (*c.gr*) which crosses the dorsal surface and runs obliquely forwards on each side to end just behind the mandible. In *Koonunga* (Fig. 95) this groove is obliterated dorsally, but a short portion persists on each side running upwards from the lower margin of the head.

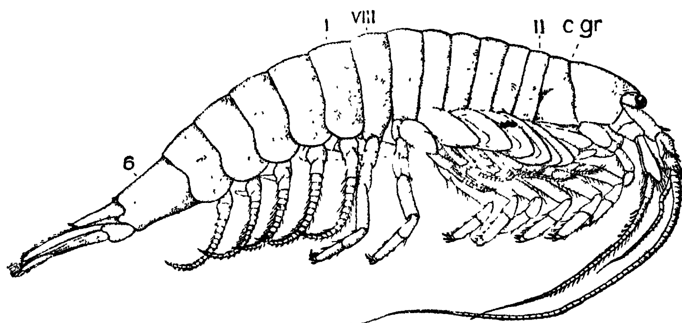


FIG. 94.

Anaspides tasmaniae, ♂, × 3. *c.gr*, "cervical groove"; II, VIII, second and eighth thoracic somites; I, 6, first and sixth abdominal somites. (Drawn by Miss G. M. Woodward.)

It has been suggested that this groove indicates the limit between the mandibular and maxillular somites and corresponds to the "cervical sulcus" of the Mysidacea, and perhaps to the transverse groove of the head in many Branchiopoda. On the other hand, a forward displacement of the lateral plates of the anterior thoracic

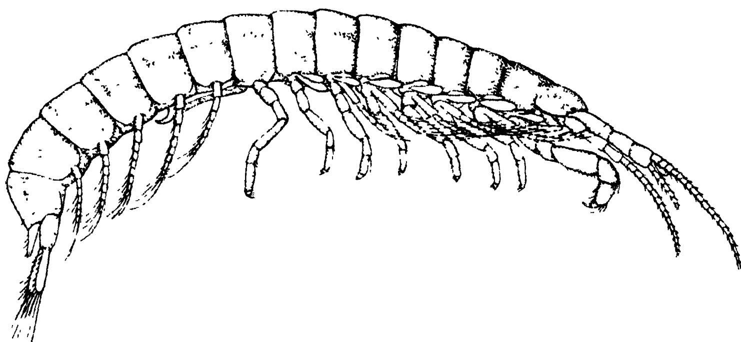


FIG. 95.

Koonunga cursor, ♂, × 11. (From an original drawing by Mr. O. A. Sayce, slightly modified.)

somites is observed in some other Malacostraca, and it is quite probable that this groove in *Anaspides* has undergone a similar displacement and that it really does define the first thoracic somite from the head. Running backwards from this groove on each side in *Anaspides* is a horizontal line marking off inferiorly a quadrilateral area.

The front of the head is produced, in *Anaspides*, into a short rostrum. On the dorsal surface, in front of the cervical groove, is a pigmented area with a circular central spot surrounded by four minute pits. The significance of this structure is quite unknown, but it may be comparable to an obscure "dorsal organ" apparently glandular in nature, occupying a similar position in certain other Malacostraca. It has not been observed in *Koonunga*.

The thoracic somites have no pleural plates and those of the abdominal somites are slightly developed. The telson, in *Anaspides* and *Koonunga*, is short, of simple form, with a fringe of spinules on the posterior margin.

Appendages.—The *antennules* are biramous, with long flagella. The first of the three segments of the peduncle contains a statocyst, opening by a narrow slit on the dorsal surface. In the male *Anaspides* the basal part of the inner flagellum is enlarged and armed with serrated spines. It appears probable that it may be used as a clasping-organ. In *Koonunga*, the antennule of the male has a curious globular organ attached to the first segment of the outer flagellum. The surface of the organ is covered with minute cup-like structures which are possibly sensory.

The *antenna* has a scale-like exopodite in *Anaspides*, but in *Koonunga* this is absent. The protopodite consists of two segments, and the first two segments of the endopodite are enlarged, so that the peduncle consists of four segments only.

The *mandibles* (Fig. 96, A) have a large palp of three segments. The serrated incisor process is separated from the molar process in *Anaspides* by a rounded lobe (*s*) fringed with setae. The lower lip is large and deeply cleft.

The *maxillula* (Fig. 96, B) has two endites and a vestigial palp. A small exite, not projecting beyond the outer edge, can be recognised.

The *maxilla* (Fig. 96, C) has three endites directed distally and crowded together, and a short, unsegmented palp. There is no exopodite.

The *thoracic limbs* are all alike in general structure. In *Anaspides* (Fig. 3, E, p. 8) the endopodite is composed of six segments (instead of the usual five) in the anterior pairs, but the articulation between the basipodite and ischiopodite becomes indistinct in passing backwards along the series, and in the last three pairs these segments have completely coalesced. In *Anaspides* the main flexure of the limb is between the fifth and sixth segments, but in *Koonunga* it appears to be between the fourth and fifth. This difference, however, is due to the fact that in all the thoracic legs of *Koonunga*, as in the posterior pairs of *Anaspides*, the basipodite and ischiopodite have coalesced. The terminal segment is small, and bears from three to five stout curved claws, one of which on the posterior legs is larger than the others.

In all except the last pair of thoracic limbs the coxopodite bears externally two ovate epipodial lamellae, each attached by a narrow base and having a small proximal segment marked off by a transverse line. These epipodites have a very thin cuticle and no doubt act as gills.

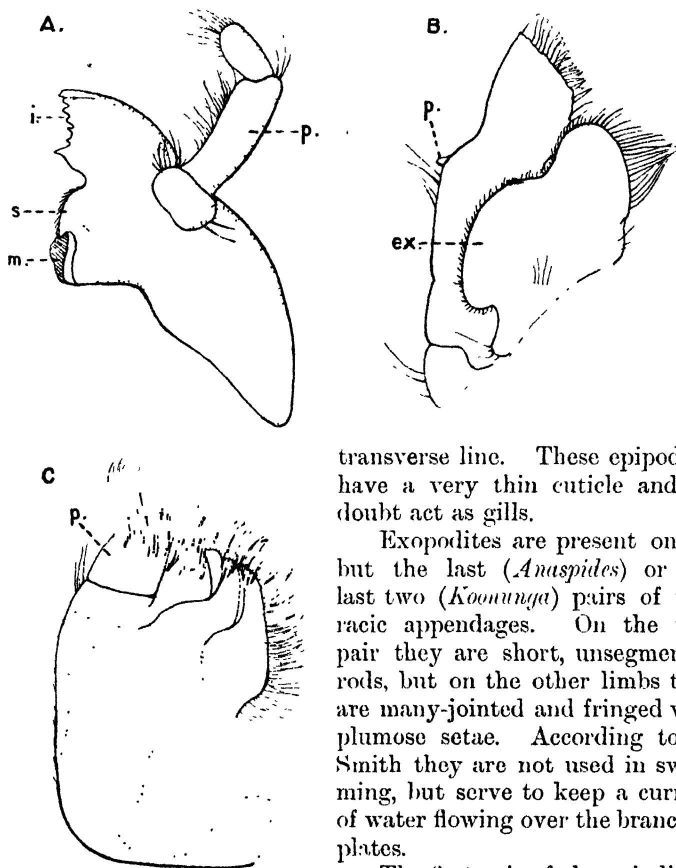


FIG. 96.

Mouth-parts of *Anaspides*. A, mandible; B, maxillula; C, maxilla. *ex*, exite; *i*, incisor process; *m*, molar process; *p*, palp; *s*, setose lobe.

Exopodites are present on all but the last (*Anaspides*) or the last two (*Koonunga*) pairs of thoracic appendages. On the first pair they are short, unsegmented rods, but on the other limbs they are many-jointed and fringed with plumose setae. According to G. Smith they are not used in swimming, but serve to keep a current of water flowing over the branchial plates.

The first pair of thoracic limbs in *Anaspides* (Fig. 3, D, p. 8) are differentiated from the others by the presence on the inner face of the coxopodite of two movably articulated gnathobasic lobes (*gn*). In *Koonunga* these lobes are wanting, but the limb differs from those which follow it in being much more stoutly built.

The *pleopods* have the exopodite long, many-jointed, and fringed with setae, forming a powerful swimming-organ. The endopodite (except in the first two pairs of the male) is small and composed of two segments in *Anaspides*, and entirely absent in *Koonunga*.

Sometimes, but not always, it is absent from the last pair also in *Anaspides*. In the males of both genera the first two pairs have the endopodites modified as copulatory organs. In the first pair of *Anaspides* the endopodite is a thick lobe, curved inwards and having a group of retinacula on a short process (perhaps a vestigial appendix interna) near the distal end of its inner edge. The endopodite of the second pair is composed of two segments, the first elongated, bearing some spines and a group of retinacula near the distal end, and the second curved and spoon-shaped. In the natural position these appendages are turned forwards, the endopodites of the second pair lying within the trough formed by the apposition of those of the first pair, and between the latter and the sternal surface of the thorax.

The *uropods* in *Anaspides* are large, with lamellar rami, fringed with spines and setae, and form, with the telson, a tail-fan of the usual type. The exopodite is crossed by an incomplete suture or line of articulation near the distal end. In *Koonunga* the protopodite is relatively longer and the rami are not so broad, so that the fan-like arrangement is not quite so typical. The exopodite is undivided.

As regards the internal anatomy, our information is as yet very restricted, and refers only to *Anaspides*.

Alimentary System.—The masticatory stomach appears to be of very simple type, its armature consisting of longitudinal chitinous ridges beset with setae. The extent of the mid-gut has not been ascertained. The hepatic caeca are numerous, very long slender tubes. There are two median dorsal caeca—one in the region of the first and the other in the fifth abdominal somite.

Circulatory System.—The heart is a long tube extending through a great part of the length of the body. The number of the ostia has not been ascertained. There is stated to be an unpaired descending artery originating from the under-surface of the heart between the last two thoracic somites.

Excretory System.—On each side of the head, posterior to the mandibles, is a glandular mass of considerable size, showing in sections a convoluted tubular structure. No duct has yet been traced from it, but its position suggests that it may be the maxillary gland.

Sense-Organs.—The paired eyes of *Anaspides* are set on short movable peduncles; those of *Koonunga* are very small and are sessile on the sides of the head.

In both genera a saccular invagination of the integument, supposed to be an otocyst (or statocyst), is found in the basal segment of the antennular peduncle. It opens by a small slit on the dorsal surface of the segment. Internally, on the upper side, is a row of peculiarly modified setae. Each is divided into two segments, the

distal one swollen and pyriform. While resembling in its position the otocyst of Decapods, this organ differs strikingly from it in the nature of the setae.

Reproductive System.—The ovaries form an elongated lobed mass on each side, extending through the posterior part of the thorax and into the abdomen. The oviducts open on the inner face of the coxopodites of the sixth pair of thoracic limbs. Between the bases of the last pair of legs on the sternal surface of the thorax is a rounded prominence directed forwards. At its tip a slit-like aperture gives entrance to a blind sac, with thick and apparently muscular walls. At the base of the sac on each side is a racemose gland, apparently opening by a short duct into its cavity. It seems probable that this structure (originally described as the opening of the oviducts) is a receptaculum seminis. A similar organ is present in *Koonunga*.

The testes are a pair of very long slender tubes, convoluted anteriorly, lying above the alimentary canal. The vasa deferentia terminate in a pair of oblique slit-like apertures on the sternal surface of the last thoracic somite.

The development, unfortunately, is still entirely unknown.

Remarks on Habits, etc.

Anaspides occurs in rocky pools at an elevation of about 4000 feet in the mountains of Tasmania. It reaches a length of about 38 mm. *Koonunga* is found in freshwater pools near Melbourne, and does not exceed 9 mm. in length.

Palaeontology.

A group of fossil Crustacea found in Carboniferous and Permian rocks in Europe and America, for which the name Syncarida was proposed by Packard, appear to be closely allied to the living *Anaspides* and *Koonunga*. The structure is best known in the case of *Uronectes* (*Gampsonyx*) (Fig. 97), described by Jordan and von Meyer from the Lower Permian of Saarbrücken. The exact number of free somites is doubtful, but there appear to be eight in the thoracic region, and there are indications that the sixth abdominal somite was divided in a manner recalling the condition found in certain Mysidacea. The eyes are pedunculated. The antennules are biramous, and the antennae have a rounded scale-like exopodite. One of the anterior pairs of thoracic limbs is enlarged and armed with stout spines. The presence of exopodites on the thoracic limbs is probable, although denied by Fritsch, but the structure of the appendages is very obscure. The uropods are lamellar, forming a tail-fan with the telson; the exopodites are

divided by a suture. In *Praeanaspides* (Fig. 98), recently described by Dr. H. Woodward from the English Coal-measures, the segmentation of the body agrees with that of *Anaspides*, and exopodites are certainly present on some of the thoracic limbs. Other genera are *Palaeocaris*, *Acanthotelson*, and *Gasocaris*.

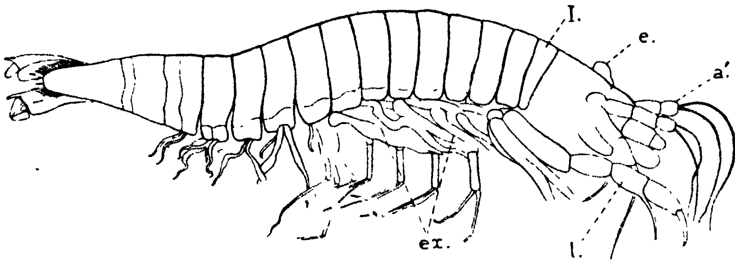


Fig. 97.

Uronectes [= *Gampsonyx*] *fimbriatus*. *a'*, antennule; *e*, supposed eye; *ex*, traces of exopodites on thoracic limbs; *l*, enlarged thoracic limb, probably the second; *I*, first thoracic somite. (After Jordan and von Meyer.)

Affinities and Classification.

The existing genera of Syncarida present characters which indicate for them a very isolated place among living Malacostraca, while suggesting more or less remote affinities with widely divergent

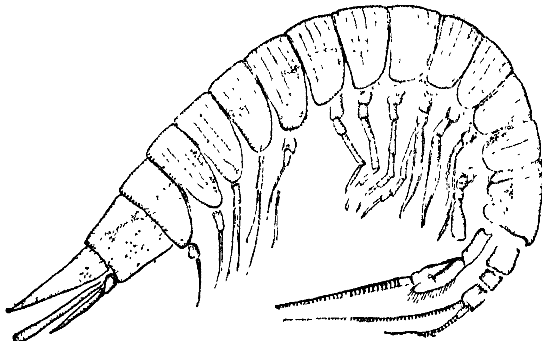


Fig. 98.

Praeanaspides praecursor, from the Coal-measures of Derbyshire. (From H. Woodward in *Geol. Mag.*)

groups. They have retained characters of the primitive caridoid type in the tail-fan, the biramous antennules, the scale-like exopodite of the antenna (in *Anaspides*), and the natatory thoracic exopodites. With the loss of the carapace, however, the segmentation of the body comes to resemble that of the Isopoda and Amphipoda, though the demarcation of the first thoracic somite from the head (if this

be indeed the significance of the "cervical groove") is not so distinct in any other Eumalacostraca. The homologies of the segments of the endopodite in the thoracic limbs are not quite clear, but the fact that the main flexure of the limb is between the fifth and sixth segments in *Anaspides* is a point of agreement with the Peracarida, to which group some slight resemblance may be traced in the structure of the maxillae. The possession of a statocyst in the basal segment of the antennule is only paralleled among the Decapoda, and the presence of a receptaculum seminis on the last thoracic sternite of the female and the modification of the first two pairs of pleopods in the male may also point to an affinity with that group. On the other hand, the double series of epipodial lamellae on the thoracic appendages of both genera, and the double gnathobasic lobes on the coxopodite of the first pair in *Anaspides*, are important features not found in any other Malacostraca.

The fossil genera mentioned above show that already in Palaeozoic times a group of Malacostraca existed which, while retaining caridoid features in tail-fan, antennules, antennae, and pedunculated eyes, had a completely segmented body and no carapace. *Anaspides* alone among living Crustacea agrees with them in this combination of characters, and there appears to be no reason to doubt that it and *Koonunga* are really descendants of the Syncarida of Carboniferous and Permian times.

Bathynella natans, to which allusion has been made, is a minute Crustacean (1·0 mm. in length), described in 1882 by Vejdovsky from two specimens found in a well in Prague. It has not since been rediscovered. It appears to possess eight free thoracic somites. There are no eyes. The antennules are uniramous, and the antennae have a small exopodite. The first seven pairs of thoracic limbs are biramous, and each has a single vesicular epipodite. The last pair are vestigial. Only the first and last abdominal somites bear appendages. If its structure has been correctly interpreted, *Bathynella* would seem to be a degenerate member of the Syncarida, but only the discovery of further specimens will enable its systematic position to be definitely fixed.

ORDER **Anaspidacea**, Calman (1904).

Family ANASPIDIDAE. *Anaspides*, G. M. Thomson. Family KOONUNGIDAE. *Koonunga*, Sayce.

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ADDENDUM.

Since this chapter was in type G. Smith has described a third living representative of the Syncarida, *Paranaspides lacustris*, from the Great Lake of Tasmania, and has given further details as to the habits and internal anatomy of *Anaspides* ("Preliminary Account of the Habits and Structure of the Anaspididae . . .," Proc. Royal Soc. (B) lxxx. pp. 465-473, pl. xiii., 1908).

CHAPTER IX

THE MYSIDACEA

Order **Mysidacea**, Boas (1883).

Definition.—Peracarida which retain more or less completely the primitive caridoid facies; the carapace extends over the greater part of the thoracic region, but does not coalesce dorsally with more than three of the thoracic somites; the eyes, when present, are movably pedunculate; the antennules are biramous; the antennae have usually a large scale-like exopodite; the thoracic limbs (except sometimes the first and second pairs) have natatory exopodites; the first and sometimes also the second pair are modified as maxillipeds; a lamellar epipodite is present on the first pair; ramified branchiae may be attached to the body-wall close to the bases of the thoracic limbs; the pleopods are often reduced; the uropods are lamellar, forming a tail-fan; the young leave the brood-pouch provided with all the appendages of the adult.

Historical.—The group Schizopoda, established by Latreille in 1817, and long approximated to the Stomatopoda on the authority of H. Milne-Edwards, finds a place in most modern systems of classification, as comprising, after exclusion of many larval Decapods formerly referred to it, the forms here treated of together with the Euphausiidae. Boas, in 1883, however, discarded this grouping, and established the two orders Mysidacea and Euphausiacea, pointing out that they were by no means closely related, and this view has been also advocated by Hansen. Our present knowledge of the structure and classification of the Mysidacea is very largely due to the work of G. O. Sars.

MORPHOLOGY.

From five to seven of the thoracic somites are distinct, and the last two or three of these may be left uncovered by the carapace on the dorsal side. The carapace may be produced in front as a short rostrum, and there is usually a transverse groove or "cervical sulcus" (Fig. 99, *c.s*) on the dorsal surface in the region of the

mandibles. The possible homology of this groove with the cervical groove of *Anaspides* has been already mentioned. The abdominal somites have the pleural plates generally reduced or absent; but in *Gastrosaccus* the pleura of the first somite are greatly enlarged in the female to help in forming the brood-pouch. The

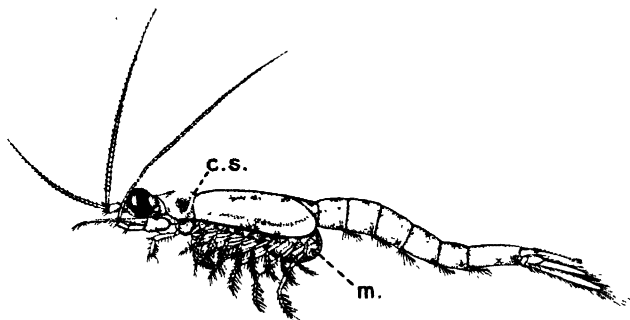


FIG. 99.
Mysis relicta, female. *c.s*, cervical sulcus; *m*, brood pouch. (After Sars.)

sixth somite is generally longer than any of the others, and in *Gnathophausia* it is divided by a transverse groove (Fig. 100, *gr*) about the middle of its length. It is possible that we have here two somites in process of coalescence, and that seven somites are represented in the abdomen of the Mysidacea as in that of the

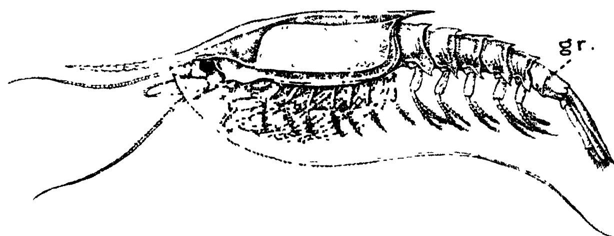


FIG. 100.
Gnathophausia willemoesii, Sars. (According to Ortmann this is the fully adult form of *G. zoea*, W. Suhm.) × ½. *gr*, groove partially dividing the last somite. (After Sars.)

Leptostraca. It is important, however, to note that the last somite in this case bears appendages (uropods) and that the penultimate does not, while in the Leptostraca the reverse is the case. The indications of a similar division of the sixth abdominal somite in certain fossil Syncarida have already been alluded to.

Appendages.—The *ocular peduncles* are peculiarly modified in many deep-sea forms in which the eyes are imperfect or absent. In *Dactylerythrops* the peduncle is produced as a finger-like process

beyond the eye; in *Boreomysis scyphops* the distal end of the peduncle is expanded and excavated in a cup-like form and is without pigment or any trace of ocular structure, but in other species of the same genus the eyes are normally developed; in some Petalophthalmidae the peduncles are leaf-like or spiniform; while in *Pseudomma*, *Amblyops*, and some allied genera, they are represented by broad plates extended horizontally in front of the carapace.

In the Mysidae the three-segmented peduncle of the *antennules* carries in the male sex, in addition to the two flagella, a conical process beset with numerous sensory filaments.

The *antennae* have the protopodite distinctly composed of three segments (Fig. 101, 1, 2, 3). A lamellar exopodite or "scale" (*sc*) is always present except in *Arachnomysis* and allied genera, where it is represented by a spine. In many Mysidae it is divided into two segments by a transverse suture near the tip.

The *mandibles* have generally a well-developed lacinia mobilis (Fig. 102, *l.m*), differing in form on the two sides, and a row of spines (*s*) interposed between the incisor and molar processes. The row of spines is absent in the Lophogastridae and Eucopiidae and some Mysidae, and in some cases the lacinia mobilis is wanting. The molar process is small or absent in a few Mysidae. A palp is always present, and becomes greatly enlarged in the aberrant *Petalophthalmus*, where it appears to have a prehensile function.

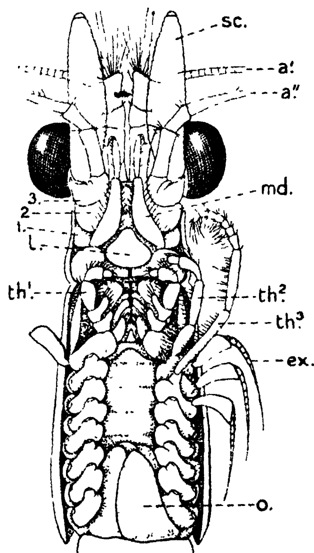


FIG. 101.

Cephalothoracic region of *Mysis relicta*, young female, from below. Most of the thoracic appendages have been removed. *a'*, external flagellum of antennule; *a''*, flagellum of antenna; *ex*, exopodites of thoracic appendages; *l*, labrum; *md*, palp of mandible; *o*, oostegites, not yet fully developed; *sc*, scale or exopodite of antenna; *th* 1-*th* 3, first, second, and third thoracic appendages; 1, 2, 3 the three segments of the protopodite of the antenna. (After Sars.).

The *maxillulae* (Fig. 103, A) have two endites arising, according to Hansen, from the first and third segments, and a slightly developed laminar exite, which Hansen states belongs to the first segment. In the genus *Gnathophausia* (Fig. 104) a palp of two segments is present, directed backwards beneath the carapace like that of the Leptostraca.

The *maxillae* (Fig. 103, B) have a complex structure. There are two endites corresponding to the second and third segments (Hansen), the first of which is incompletely and the second com-

pletely divided into two. A plate-like lobe on the outer side (*f*) is regarded as the exopodite and springs from the third segment (Hansen). The palp is composed of two segments. In *Gnathophausia* a pigmented papilla on the outer side close to the base bears the opening of a gland producing a luminous secretion.

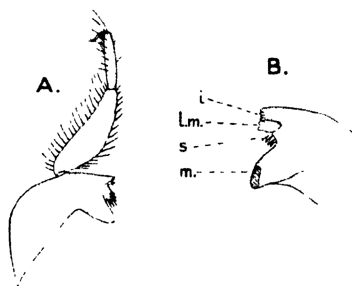


Fig. 102.

A, mandible of *Mysis*. B, oral edge of same, further enlarged: *i*, incisor process; *l.m.* lacinia mobilis; *m*, molar process; *s*, spine-row. (A after Sars.)

The *thoracic appendages* have the coxopodite very small, and have usually an exopodite consisting of a peduncle and a multi-articulate setose flagellum attached near the proximal end of the basipodite. The exopodites of the first pair may be reduced (Lophogastridae, Eucopiidae) or absent (some species of *Gnathophausia*, Petalophthalmidae), and those of the second pair are absent in *Petalophthalmus*.

The first pair of thoracic limbs are always specialised as maxillipeds. In the Lophogastridae and Eucopiidae they are without distinct endites. In the Mysidae (Fig. 105, A) an endite is generally borne by the basipodite, and sometimes also by each of the two following segments. In *Petalophthalmus* the first and second thoracic limbs (in the other genera of Petalophthalmidae only the second) have a large lamellar endite developed from the meropodite.

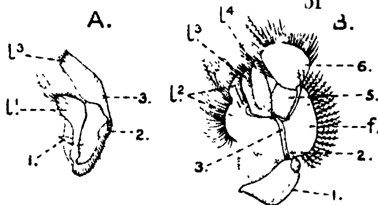


Fig. 103.

A, maxillula, B, maxilla, of *Mysis oculata*. 1-6, segments of the appendages; *l1*-*l4*, endites of the respective segments according to Hansen's earlier interpretation (in his later papers the endites here numbered 3 and 4 in the maxilla are regarded as resulting from the division of a single endite corresponding to the third segment, and the segments here numbered 5 and 6 become 4 and 5 respectively); *f*, flabellum or exopodite. (After Hansen.)

In the Lophogastridae (Fig. 106) the last seven pairs of thoracic limbs are all similar, and exhibit the usual number of seven segments, the dactylus being large and having generally a claw-like spine at the apex. In the Eucopiidae the second to the fifth pairs are subchelate, and the next three pairs, which are exceedingly long and slender, have also the dactylopodite flexed against the propodite to form a prehensile organ. In the Mysidae there is, as a rule, a distinction between the second and the following limbs. The former, sometimes called second maxillipeds or "gnathopoda," are bent inwards towards the mouth, with the normal number of segments and with a rounded dactylopodite

without a claw. The remaining pairs (Fig. 105, B) have the propodite (except in most Petalophthalmidae and some species of *Siriella*) divided into secondary segments from two (*Boreomysis*, *Siriella*) to eight or nine in number. The dactylopodite is usually small, and terminates in a claw-like spine. In *Heteromysis* the third pair are enlarged and prehensile.

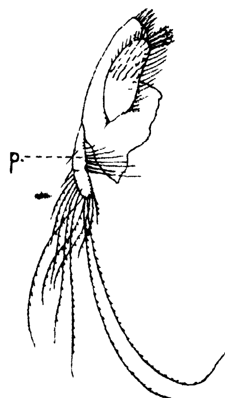


Fig. 104.
Maxillula of *Gnathophausia longispina*. *p*, palp. (After Sars.)

In all Mysidacea the first pair of thoracic limbs have a simple lamellar *epipodite* (Fig. 105, A, *ep*) directed backwards beneath the carapace. In the Lophogastridae and Eucopiidae a series of ramified *gills* (Fig. 106, *br*) are developed in connection with the last seven thoracic limbs. Each consists of three or four main branches, which are again bipinnately or tripinnately divided. The largest branch is bent round on the sternal surface of the thorax between the insertion of the limbs, a point of some interest in connection with the position of the gills in the Amphipoda. Although the gills of the Lopho-

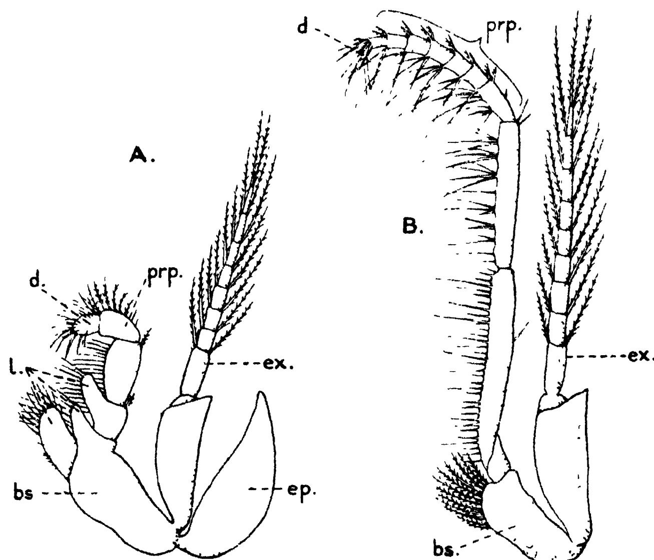


Fig. 105.
A, first thoracic appendage (maxilliped) of *Mysis*. B, third thoracic appendage of same. The minute coxopodite is omitted in each case. *bs*, basipodite; *d*, dactylopodite; *ep*, epipodite; *ex*, exopodite; *l*, masticatory lobes or endites of basipodite, ischiopodite, and meropodite; *prp*, propodite, divided into seven segments in B. (After Sars.)

gastridae and Eucopiidae are attached to the body-wall or to the articular membrane rather than to the coxopodites of the limbs, it is probable that they are really of the nature of epipodites. In *Gnathophausia* a short finger-like process bearing long setae is found on the outer side of the coxopodite, and apparently represents a reduced distal epipodite (Fig. 106, *ep*). In the Mysidae and Petalophthalmidae there are no epipodites on the limbs posterior to the first thoracic pair, apart from some vestiges described in *Euchaetomera* and allied genera. Seven pairs of *oostegites* are found attached to the coxopodites of all except the first pair of thoracic appendages in the females of the Lophogastridae, Eucopiidae, and Petalophthalmidae, and in the genus *Boreomysis* among the Mysidae. In the other Mysidae the number does not exceed three pairs, and it is often reduced to two, corresponding to the last two thoracic somites (Fig. 101, *o*).

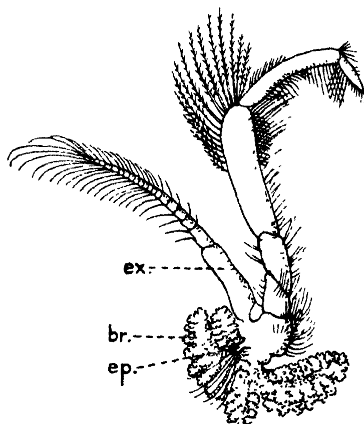


FIG. 106.

Second thoracic appendage of *Gnathophausia longispina*. *br*, branchia; *ep*, epipodial process; *ex*, exopodite. (After Sars.)

The *pleopods* are well developed in both sexes in the Lophogastridae and Eucopiidae, where they have multiarticulate rami fringed with setae, and no special modifications are found in either sex. In the Petalophthalmidae and Mysidae the pleopods are vestigial in the female (except in the little-known *Archaeomysis*), but are often well developed in the male. When they are reduced in the latter sex some of the pairs, most commonly the fourth, are specially modified. In the males of some Mysidae the peduncle bears distally, in addition to the two rami, a lobe or process of varying form, to which a branchial function has been attributed.

The *uropods* have the exopodite divided into two segments by a transverse suture in the Lophogastridae, Eucopiidae, and Petalophthalmidae, and, less distinctly, in certain Mysidae. A statocyst is present near the base of the endopodite in most Mysidae, but it is absent or vestigial in *Boreomysis* and in the other families.

Alimentary System.—The stomach in *Mysis* (Fig. 107, *st*) is divided into a globular cardiac portion occupying the greater part of the cavity of the head in front of the cervical sulcus and a much smaller pyloric portion. The interior of both chambers has numerous ridges and prominences armed with spines and setae. In particular, a tongue-shaped process directed backwards on the

floor of the pyloric division, and bearing on each side anteriorly a double comb-like row of iridescent setae, can be identified with a similar process found in Amphipoda and Isopoda. The extent of the mid-gut does not seem to have been determined. Five pairs of hepatic caeca (Fig. 107, *hep*) are found in *Mysis*, opening by a common duct on each side just behind the tongue-shaped process on the floor of the pyloric chamber. Two pairs are very short and directed forwards; of the three pairs directed backwards, the upper and lower extend through the greater part of the thorax while the middle pair are much shorter. In *Siriella* there are only three pairs, one turned forwards and two longer pairs turned backwards. An unpaired dorsal diverticulum (*d*) is given off at the junction of stomach and intestine.

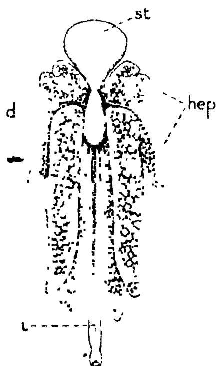


FIG. 107.

Alimentary canal of *Mysis*. *d*, dorsal diverticulum; *hep*, hepatic caeca; *i*, intestine; *st*, cardiac chamber of stomach (After Sars.)

Circulatory System.—The heart of the Mysidae is elongated, fusiform, extending the whole or the greater part of the length of the thoracic region. There are only two pairs of ostia, one dorsal to and slightly in advance of the other. Anteriorly and posteriorly the heart is continued into median aortic vessels each flanked at its origin by a pair of lateral vessels. From the under-side of the heart a number of median vessels are given off to the underlying viscera, and near the posterior end there originates an unpaired descending artery which passes on one side of the intestine. On approaching the sternal surface it divides in the median plane into three branches which pass between the connectives of the nerve-chain in the fifth, sixth, and seventh thoracic somites. The anterior branch is continued forwards as a subneural artery through the anterior thoracic somites; the middle branch supplies the sixth and the posterior the seventh and eighth somites and their limbs. The abdominal aorta gives off in each somite, besides paired vessels which terminate in the pleopods, a median branch which passes on one side of the intestine and runs for a little way alongside the ventral nerve-cord, sometimes anastomosing with its neighbours in front and behind. The interest of this disposition of the arterial trunks lies in the fact that the descending artery given off from the posterior end of the heart, which is clearly homologous with the similar vessel found in the Decapoda, is here seen to be one of a series of median vessels originating from the under-side of the heart and of the abdominal aorta, and contributing to the formation of a discontinuous sternal or subneural vessel on the ventral side of the body.

Fine capillary networks surround and penetrate the optic ganglia and those of the thoracic region. Converging venous channels on the sides of the thorax convey the blood from the limbs to the pericardium. Small papilliform elevations of the integument on the course of these channels in *Mysis* have been credited with a branchial function. The chief seat of respiration in the Mysidae, however, appears to be the carapace, in which is a rich network of blood-channels receiving blood from the sinuses of the anterior part of the body and returning it to the pericardium. The epipodite of the maxilliped may also have a branchial function, and at all events serves, by its movements, to maintain a current of water under the wings of the carapace. The branchiae of the Lophogastridae and Eucopiidae have already been described.

Excretory System.—The antennal gland is well developed in *Mysis*. The canal is much convoluted and expands into a small bladder before opening to the exterior on the second segment of the antennal peduncle. Groups of excretory cells are present also at the bases of the thoracic limbs.

Nervous System.—The oesophageal connectives are elongated and a post-oesophageal (antennal) commissure appears to be present. In *Boreomysis* the full number of eleven pairs of ganglia can be distinguished in the cephalothoracic part of the ventral chain, but in *Mysis* all are coalesced into a continuous mass within which only ten pairs of ganglia can be made out. In *Gnathophausia* the first three pairs are completely coalesced and the fourth is closely approximated to them, but the remaining seven pairs are distinct. In all cases six abdominal ganglia are present.

Sense-Organs.—The eyes have the cornea slightly faceted externally. The crystalline cone is bipartite and the elongated rhabdome is quadripartite. In certain bathypelagic Mysidae the ommatidia are divided into two groups differing in structure. In *Gnathophausia* there is, on the upper surface of the ocular peduncle, a small prominence which probably corresponds to the sensory papillae found in the Leptostraca.

The statocyst, which is found in the endopodite of the uropods in nearly all Mysidae (Fig. 108), consists of a spacious vesicle originating as an invagination of the integument and remaining in communication with the exterior (in some species at least) by a narrow fissure. It contains a single large discoidal statolith (*st*), consisting of an organic nucleus surrounded by a thick shell of calcium fluoride and resting on a group of setae springing from the floor of the cavity. The tips of the setae are imbedded in the substance of the statolith. Each statocyst is supplied by a large nerve (*n*) from the last pair of abdominal ganglia.

Holt and Tattersall have observed in *Hansenomysis* a pit on the upper surface of the proximal segment of the antennule. Although

no sensory setae could be discovered, it seems possible that this pit may represent the antennular statocyst of Syncarida and Decapoda.

Reproductive System.—The two tubular ovaries are connected with each other by a narrow bridge. The oviducts proceed from their hinder ends and probably open in the usual position at the base of the sixth thoracic limbs. The testes are closely approximated in the middle line and consist each of a number of pyriform follicles opening into the vas deferens, which is dilated near the front of each testis to form a seminal vesicle. The external openings are situated on papilliform elevations at the bases of the last pair of thoracic limbs. The spermatozoa have the form of slender rods each with a filiform tail attached at an acute angle at one end.

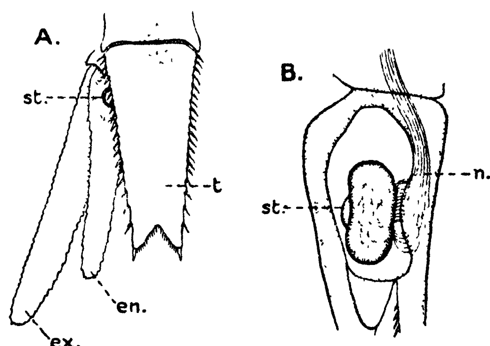


Fig. 108.

A, telson and one uropod of *Mysis*, from above. The marginal setae of the uropod are omitted. B, the statocyst, seen in optical section from the side further enlarged. *en*, endopodite of uropod, containing the statocyst near its base; *ex*, exopodite of uropod; *n*, nerve supplying sensory setae of statocyst; *st*, statolith; *t*, telson. (After Sars.)

Development.—The whole course of development takes place within the brood-pouch. In the Mysidae segmentation is of the discoidal type. The embryo becomes freed from the egg-membrane after the appearance of the first three pairs of appendages, at which stage, corresponding to the nauplius, the first larval cuticle is formed (Fig. 109). The caudal region, which within the egg was flexed ventrally, becomes extended and the body acquires a slight dorsal curvature. An important feature is the presence of two immovable setose styles (*f*) terminating the abdomen and representing the caudal furca of the Leptostraca. Under the cuticle of this maggot-like nauplius stage the remaining cephalic and thoracic appendages (*th*) appear simultaneously, followed by the uropods and, after an interval, by the pleopods. The elongation of the body in the post-naupliar region is effected by successive divisions of a series of teloblastic cells as in Isopoda. A pair of lateral

thickenings of epiblast appear very early and, approaching each other on the dorsal side, fuse to form an invaginated "dorsal organ" (*d*). The young animal leaves the brood-pouch with all the appendages developed.

Advanced embryos closely similar to those of the Mysidae have been observed in *Lophogaster* and *Eucopia*.

Remarks on Habits, etc.

The great majority of Mysidacea are marine, but a few Mysidae occur in fresh water either as apparently recent immigrants from the sea, or as "relict" forms like the *Mysis relicta* (Fig. 99) found in lakes in Northern Europe, Ireland, and North America. A few Mysidae are members of the surface plankton, and a number of peculiarly modified genera of that family, like all the members of the other families, are bathypelagic at great depths.

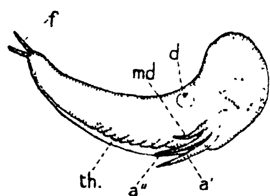


Fig. 109.

Embryo of *Mysis* (*Macromysis*). *a'*, antennule; *a"*, antenna; *d*, dorsal organ; *f*, caudal furca; *md*, mandible; *th*, thoracic limbs. (After Nusbaum.)

Most of the Mysidae are of small size, few approaching *Boreomysis scyphops*, which reaches 85 mm. in length; on the other hand, *Anchialus pusillus* is only 3 mm. long. Among the Lophogastridae many species are of considerable dimensions, and *Gnathophausia ingens*, the largest member of the order, reaches a length of 157 mm.

Palaeontology.

The genus *Pygocephalus* was established by Huxley in 1857 for a species occurring in the Coal-measures of Scotland which he compared with the existing genus *Mysis*. Dr. H. Woodward has recently made the highly important discovery that *Pygocephalus* possessed a brood-pouch formed by six or seven pairs of imbricating oostegites (Fig. 110), thus showing that it must be classed with the Peracarida. *Pygocephalus* has a broad and apparently flattened body, with a carapace covering the thoracic region. The antennules are biramous and the antennae have a broad scale-like exopodite. Seven pairs of thoracic limbs are visible in the fossils (the first pair were probably folded inwards as maxillipeds and are therefore invisible), carrying each a multiarticulate exopodite. The uropods and telson form a broad tail-fan. This combination of caridoid and Peracaridan characters justifies us in assigning *Pygocephalus* a place among the Mysidacea, although it is impossible at present to define more precisely its relation to the existing families of the order. It is not known whether the tergal portions of any of the thoracic

somites were distinct beneath the carapace in *Pygocephalus*, but in the genus *Crangopsis* of Salter, from the Lower Carboniferous, Ortmann has shown that at least four somites are distinct. It is probable that other fossil genera, such as the Carboniferous *Anthrapalaemon*, may be found to possess Mysidacean characters.

AFFINITIES AND CLASSIFICATION.

The removal of the Mysidacea from their old association with the Euphausiidae in the group "Schizopoda" is justified by the fact that the two groups do not have in common any characters except those of the primitive caridoid facies which they share with the lower Decapoda and, in part, with the Stomatopoda. On the other hand, the connection of the Mysidacea, through the Cumacea and Tanaidacea, with the Isopoda and Amphipoda is shown not only by the characters given in the definition of the division Peracarida, but also by many connecting characters which link together the individual orders. For example, the retroverted palp of the maxillula in *Gnathophausia* is repeated in the Cumacea and Tanaidacea, and the branchial epipodite of the first thoracic limb in these two orders may be derived from the simpler appendage found in the Mysidacea.

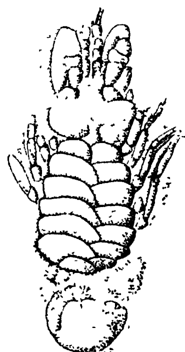


FIG. 110.
[illegible], from the Coal Measures. Female specimen, from below, showing the imbricated oostegites. (After Woodward.)

The families mentioned below are those accepted by G. O. Sars, with the addition of the Petalophthalmidae, established by Holt and Tattersall (following Czerniavsky). The sub-families of the Mysidae as adopted here have been regarded by Norman as distinct families.

ORDER **Mysidacea**, Boas (1883).

Family LOPHOGASTRIDAE. *Lophogaster*, M. Sars; *Gnathophausia*, Willemoes-Suhm (Fig. 100). Family EUCOPIIDAE. *Eucopia*, Dana. Family PETALOPHTHALMIDAE. *Petalophthalmus*, Willemoes-Suhm; *Hansenomysis*, Stebbing. Family MYSIDAE. Sub-Family ARCHAEOMYSINAE. *Archaeomysis*, Czerniavsky. Sub-Family LEPTOMYSINAE. *Leptomysis*, G. O. Sars; *Erythrops*, G. O. Sars; *Dactylerythrops*, Holt and Tattersall; *Euchaetomera*, G. O. Sars; *Amblyops*, G. O. Sars; *Pseudomma*, G. O. Sars. Sub-Family ARACHNOMYSINAE. *Arachnomysis*, Chun. Sub-Family MYSIDETINAE. *Mysidetes*, Holt and Tattersall. Sub-Family MYSINAE. *Mysis*, Latreille (Fig. 99); *Macromysis*, White (= *Praunus*, Leach). Sub-Family STILOMYSINAE. *Stilomysis*, Norman. Sub-Family HETEROMYSINAE. *Heteromysis*, S. I. Smith. Sub-Family MYSIDELLINAE. *Mysidella*, G. O.

Sars. Sub-Family SIRIELLINAE. *Siriella*, Dana. Sub-Family GASTROSACCINAE. *Gastrosaccus*, Norman; *Anchialus*, Kroyer (= *Anchialina*, Norman and Scott). Sub-Family BOREOMYSINAE. *Boreomysis*, G. O. Sars.

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CHAPTER X

THE CUMACEA

Order **Cumacea**, Kröyer (1846).

Definition.—Peracarida in which the carapace coalesces dorsally with the first three or four thoracic somites, overhangs on each side to enclose a branchial cavity, and is produced in front into two plates which usually meet each other above in front of the head to form a pseudorostrum; the telson may be coalesced with the last somite; the eyes are generally coalesced into a single organ set on an immovable process of the head; the antennules may be biramous; the antennae have no exopodite; some of the thoracic limbs have natatory exopodites; the first three pairs are modified as maxillipeds; the first pair have an epipodite generally provided with branchial lobules and an exopodite forming a respiratory siphon; the pleopods are absent in the female and often reduced in the male; the uropods are styliform; the young leave the brood-pouch before the appearance of the last pair of thoracic limbs.

Historical.—The first described Cumacean was the *Oniscus scorpioides* of Lepechin (1779), and other species were described by Montagu (1804), Say (1818), and H. Milne-Edwards (1828). The last-named author established the genus *Cuma*, from which the name of the order is derived, but he later regarded this as being a larval decapod, and he maintained his opinion of the larval nature of the group as late as 1858, although Kröyer had described ovigerous females in 1841 and his discovery had been confirmed by H. Goodsir and others. While Spence Bate, Norman, Lilljeborg, Hansen, Dohrn, and others have contributed descriptions of species and observations on structure and development, by far the greater part of our present knowledge of the group is based on the elaborate and beautiful memoirs of G. O. Sars.

MORPHOLOGY.

The general shape of the Cumacea is usually very characteristic, owing to the sharp distinction between the inflated cephalothoracic

region and the slender and very mobile abdomen carrying at its tip the styliform uropods (Fig. 111). The extreme specialisation of the respiratory system, with the concomitant modification of the anterior part of the carapace, are the most striking features differentiating this from the neighbouring orders. As in the Mysidacea and Tanaidacea the first thoracic limb (maxilliped) carries a backwardly directed membranous epipodite lying in a cavity between the carapace and the side wall of the body; but in the Cumacea this epipodite is of relatively great size, and is usually (though not always) furnished with respiratory processes or lamellae (Fig. 112, *br*), which may be very numerous and are often better developed in the more active males than in the females. Anteriorly, the branchial cavity is continued as a narrow channel covered by a forward extension of the lateral plate of the carapace,

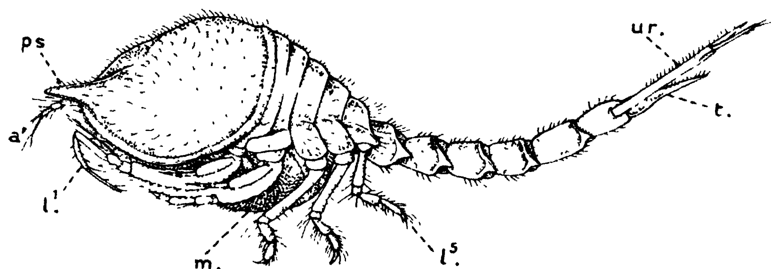


FIG. 111.

Diastylis Goodsiri, ♀, from the side × 4. *a'*, ant [illegible] fifth legs (fourth and eighth thoracic appendages); *m*, brood-pouch; [illegible] son; *ur*, uropod. (After Sars.)

the two lateral plates generally meeting each other above in front of the head and forming a more or less prominent *pseudorostrum* (*ps*) divided by a Y-shaped fissure (Fig. 112, *fr*). Within this channel lies the exopodite of the same appendage in the form of a narrow stalk bearing distally a membranous expansion, which is rolled upon itself to form a tube, or unites with its fellow of the opposite side in a single tube (*ex*) capable of protrusion from the front of the head below the pseudorostrum. Sometimes the pseudorostral plates do not quite meet in front of the head, and in certain genera (*Zygosiphon*) these plates, and the respiratory channels which they cover, are placed wide apart at the sides of the broadly expanded frontal region, while the exopodal tubes project as long transparent siphons.

Eyes are altogether deficient in many genera. When present they are usually coalesced to form a single median organ (Fig. 112, *e*) borne on the front of the head, which is produced into an oculiferous lobe lying between the two plates of the pseudorostrum.

When the lateral plates are removed, the conformation of the head and the position of the eye show some similarity to the arrangement met with in the Oedicerotidae among the Amphipoda. The two eyes are distinct in the embryo, and in one genus (*Nannastacus*) also in the adult.

Appendages.—The *antennules* rarely have both flagella well developed, the inner being usually reduced or absent. The *antennae* differ remarkably in the two sexes. In the female (Fig. 112, *a''*) they are vestigial, while in the male they consist of a stout peduncle of five segments, of which the last two are enlarged and clothed with a brush of long setae, while the flagellum is filiform and may exceed the length of the body (Fig. 113). In life this long flagellum is usually carried folded close to the side of the body, protected by the lower edge of the carapace and by the pleural plates of the abdomen, or in a special groove which runs along the sides of the abdominal somites. In the genus *Lamprops* the antennal flagella of the male are short and stout, and are used as clasping-organs to hold the female.

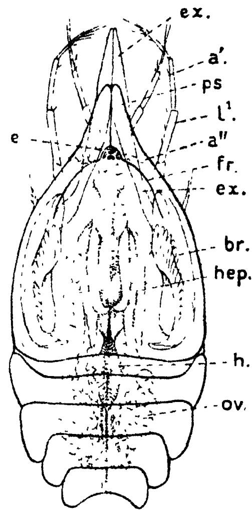


FIG. 112.

Diagram of anterior part of body of *Diastylis*, ♀, from above, showing the internal organs. *a'*, antennule; *a''*, antenna; *br*, branchial epipodite of first maxilliped enclosed in branchial cavity at side of carapace; *e*, eyes, coalesced into one; *ex*, exopodite of first maxilliped, forming the respiratory siphon; *fr*, lateral branch of 'frontal fissure' between the head and the lateral plate of pseudorostrum; *h*, heart; *hep*, hepatic caeca; *l*¹, first pair of legs; *ov*, ovary; *ps*, pseudorostrum. (After Sars.)

The *mandibles* never carry a palp, but in other respects conform to the type characteristic of the Peracarida. In the Leuconidae and in the genus *Diastyloides* the body of the mandible is short and triangular and the row of spines is reduced. In *Campylaspis* the molar process is styliform.

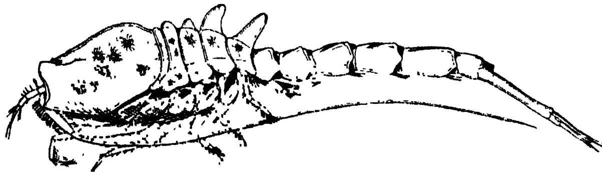


FIG. 113.

Pterocuma pectinatum, ♂, from the Caspian Sea. (After Sars, from *Ency. Brit.*)

The *maxillulae* (Fig. 114, A), except in *Platyaspis* and *Paralamprops*, carry a retroverted palp as in Tanaidacea and Lophogastridae. The *maxillae* (Fig. 114, B) with their two terminal

endites present a close approximation to those of Tanaidacea and Isopoda. In *Campylaspis* the endites are suppressed.

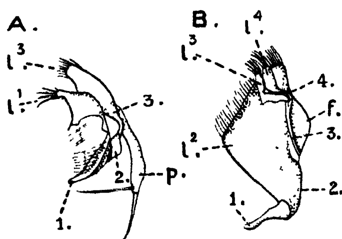


FIG. 114.

A, maxillula, B, maxilla, of *Diastylis Goodsiri*. 1-4, segments of the appendages; l^1-l^4, endites of the respective segments; *f*, flabellum (exopodite): *p*, palp. According to Hansen's later interpretation, the chitinous piece here numbered 4 in the maxilla does not represent a distinct segment, and the endites l^3 and l^4 result from the division of a single endite belonging to the third segment. (After Hansen.)

The first *thoracic appendages* with their respiratory epipodites (Fig. 115) have a close resemblance to those of the Tanaidacea, in which group, however, there is no exopodite. The basipodite has an endite directed distally, and carries on its inner edge two or three hooked spines ("coupling-hooks") which interlock with those of the other side. The second and third thoracic limbs, though less specialised, may also be reckoned as maxillipeds, since they are turned forwards and applied to the oral region with their basipodites flattened and meeting in the middle line, while the terminal segments are relatively weak and carried in a folded position. The second pair are without exopodites, but in the female a small scale bearing a fan-like fringe of setae is attached behind to the base of the limb, projecting backwards into the marsupial chamber and serving to keep in motion the eggs or embryos contained therein. This scale is doubtless homologous with the *oostegites*, which are well developed on the four succeeding pairs of limbs, where they are firmly attached to the small coxal segments. The third pair are only rarely devoid of exopodites. The fourth pair of thoracic limbs are long raptorial or prehensile *legs* (Fig. 111, l^1), though their broad basipodites, sometimes meeting in the middle line, are not dissimilar to those of the preceding pair. The fifth pair (2nd legs) often have a reduced number of joints and differ in details from the succeeding three pairs, which are all similar and appear to be fossorial in function. The small terminal segment in these limbs is tipped with a comparatively weak spine, which only in the Nannastacidae becomes a stout curved claw. Natatory exopodites are always present on the fourth pair (1st legs), and usually on one or more of the succeeding pairs in the female sex; in the

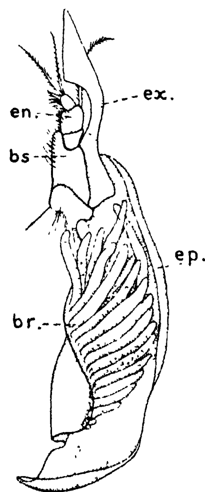


FIG. 115.

First maxilliped of *Diastylis stygia*. *bs*, basipodite; *br*, branchial lamellae on epipodite; *en*, endopodite; *ep*, epipodite; *ex*, exopodite, forming the respiratory siphon. (After Sars.)

males (Fig. 113) they are generally present on all save the last pair of legs.

The *pleopods* are always absent in the female and sometimes in the male, but more usually in the latter sex from one to five pairs are well developed and biramous. The *uropods* are always conspicuous, their slender rami furnished with comb-like rows of spines apparently used in cleaning the anterior appendages, for which purpose the abdomen can be flexed ventrally and sometimes also dorsally.

Internal Anatomy.—The masticatory *stomach* is stated to resemble closely that of the Tanaidacea. There are from one to four pairs of *hepatic caeca* (Fig. 112, *hep*). In one genus (*Platycuma*) the anterior part of the intestine is coiled, forming a spiral of two and a half turns within the carapace, but it has not been ascertained whether the coiled part belongs to the mesenteron or to the proctodaeum. In this genus also the hepatic caeca appear to be absent. The *heart* (*h*) is usually somewhat elongated, but in *Platycuma* it is subglobular. There are three pairs of ostia. Besides anterior and posterior median arteries, the heart gives off a pair of antero-lateral vessels and an unpaired descending artery. A well-developed *maxillary gland* is present, which, according to Claus, resembles closely that of *Apseudes* (Tanaidacea). The ventral *nerve-chain* consists of ten thoracic and six abdominal ganglia.

The simple tubular paired *ovaries* are connected, at least in the young, by a narrow transverse bridge. The openings of the oviducts have not been seen. The *testes* are separate, tubular, with four small caeca anteriorly. The short vasa deferentia open on the sternal surface of the last thoracic somite.

Development.

The development appears to resemble, in its main features, that of the Isopoda. In the earlier stages the embryo is curved dorsally. As in the Tanaidacea and Isopoda, the young leave the brood-pouch with the last pair of legs still undeveloped. In certain species this deficiency persists very late, and possibly in some cases throughout life.

Remarks on Habits, etc.

The Cumacea are exclusively marine (including under this term the group of peculiar species inhabiting the Caspian Sea), and are generally found burrowing in sand or mud. No species appears to be truly pelagic, although the actively swimming males of some species, and less commonly the females, are found in the plankton

of inshore waters. In Arctic seas the Cumacea are conspicuous by their abundance and relatively large size, but they are also common in suitable localities in tropical waters. Many species, often also of considerable size, occur in the deep sea.

The thirteen species known from the Caspian Sea all belong to the family Pseudocumidae, and were originally referred to the single genus *Pseudocuma*, which comprises only three truly marine species. It is interesting to note that several of the Caspian species "mimic" in their general aspect widely different genera of other families, and have on this account received such specific names as *diastyloides*, *eudorelloides*, and *campylaspoides*.

The largest known Cumacean is the Arctic *Diastylis Goodsiri* (Fig. 111), which reaches a length of 35 mm. Some deep-sea species are not much inferior to this, but the average size is much less, and some species do not exceed 1·5 mm. in length.

No fossil Cumacea are known.

Affinities and Classification.

The systematic position of the Cumacea has been somewhat obscured by the customary classification of the Malacostraca into Edriophthalma and Podophthalma, since they unite the sessile eyes of the former group with the carapace of the latter. As a matter of fact, apart from characters of specialisation which seem to have arisen within the order, they clearly stand midway between the Mysidacea and the Tanaidacea, just as they combine, to some extent, the swimming powers of the one with the burrowing habits of the other.

Order **Cumacea**, Kröyer (1846).

Family Bodotriidae. *Bodotria*, Goodsir (= *Cuma*, H. Milne-Edwards); *Cyclaspis*, G. O. Sars; *Zygosiphon*, Calman. Family Vauntompsoniidae. *Vauntompsonia*, Spence Bate. Family Leuconidae. *Leucon*, Kroyer; *Eudorella*, Norman. Family Nannastacidae. *Nannastacus*, Spence Bate; *Campylaspis*, G. O. Sars; *Platycuma*, Calman. Family Ceratocumidae. *Ceratocuma*, Calman. Family Pseudocumidae. *Pseudocuma*, G. O. Sars; *Pterocuma*, G. O. Sars (Fig. 113). Family Lampropidae. *Lamprops*, G. O. Sars; *Paralamprops*, G. O. Sars. Family Platyaspidae. *Platyaspis*, G. O. Sars. Family Diastylidae. *Diastylis*, Say (Fig. 111); *Diastyloides*, G O. Sars.

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CHAPTER XI

THE TANAIDACEA

Order **Tanaidacea**, Hansen (1895).

Definition.—Peracarida in which the carapace coalesces dorsally with the first two thoracic somites, and overhangs on each side to enclose a branchial cavity; the telson is not defined from the last somite; the eyes, when present, are usually set on short, immovable peduncles; the antennules may be biramous; the antennae may have a small exopodite; vestigial exopodites are sometimes present on the second and third pairs of thoracic limbs; the first pair of thoracic appendages are modified as maxillipeds; they have an epipodite lying in the branchial cavity, but no exopodite; the second pair are chelate; the pleopods are usually present and biramous; the uropods are slender; the young leave the brood-pouch before the appearance of the last pair of thoracic limbs.

Historical.—The first known member of this order was that described by Montagu in 1808 as *Cancer gammarus talpa*, now placed in the genus *Apseudes.* Leach, Latreille, and others ranked the species known to them among the Amphipoda, while H. Milne-Edwards placed them among the Isopoda, remarking, however, that they established a transition to the Amphipoda. Dana (1852) united them with certain parasitic and other Isopoda in a group Anisopoda interposed between Isopoda and Amphipoda, and Spence Bate in 1868 combined them with the Isopod Anthuridae and Anceidae (Gnathiidae) in a no less heterogeneous group of "Isopoda aberrantia." Van Beneden (1861) called attention to the importance of the carapace of *Tanais* as a systematic character, and approximated that genus to *Cuma* and *Mysis.* F. Müller (1864) also attached great weight to the same character. Gerstaecker (1886) once more included the Tanaidacea among the Amphipoda; but this retrograde step has met with little support, and most modern writers follow Sars in ranking them as one of the tribes of Isopoda (Chelifera). Claus, however, in 1888 placed them in an independent order, for which he adopted Dana's name Anisopoda,

and which he placed between Isopoda and Cumacea. Hansen adopts the same view of their affinities, and suggests for the order the name which is here used. Claus's monograph on *Apseudes* is the most important source of information on the anatomy of the group, and the works of G. O. Sars are no less important as regards the description and classification of genera and species.

Morphology.

The general form of the body (Fig. 116) resembles that typical of the Isopoda, being depressed or sub-cylindrical, with a comparatively short abdominal region and with the telson coalesced with the last somite. The homology of the reduced carapace with that of the Cumacea and Mysidacea is indicated by the small cavity which it overhangs on each side and within which lies the epipodite of the first thoracic appendage. Only the first and second thoracic

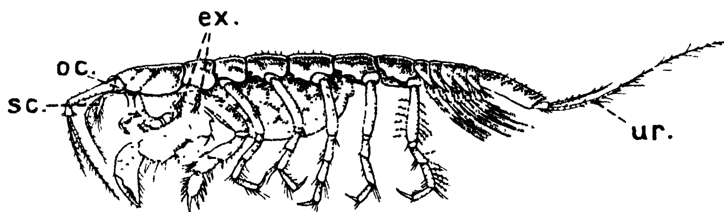


Fig. 116.

Apseudes spinosus, female. *ex*, vestigial exopodites of second and third thoracic limbs; *oc*, ocular lobe or peduncle; *sc*, scale (exopodite) of antenna; *ur*, flagelliform uropod. (After Sars.)

somites are coalesced with the carapace, but in *Sphyrapus* the third somite is firmly attached to the head-region, although, according to Sars, it is not completely fused with it.

The eyes are often absent, but when present they are usually set on fronto-lateral processes of the head (Fig. 116, *oc*), which in many species are defined by grooves and, although not movable, appear to correspond to the ocular peduncles of the podophthalmate groups.

Appendages.—The *antennules* are biramous in the Apseudidae. In some species the two flagella are stated to arise from a common basal segment, so that the peduncle consists of four segments. The *antennae* have, in the Apseudidae, a small exopodite (Fig. 116, *sc*), and the protopodite consists of two segments, not, as is usual in the Peracarida, of three. The *mandible* carries a palp in the Apseudidae, but not in the Tanaidae. The *maxillulae*, in the former family (Fig. 117, B), have two endites and a palp of two segments, but in the Tanaidae the proximal endite is wanting and the palp is unsegmented. The *maxillae* of the Apseudidae (Fig. 117, C)

have a small palp. In the Tanaidae the whole appendage is vestigial. The *lower lip* of the Apseudidae (Fig. 117, A) is peculiar in having each of the lobes terminating in a movably articulated lappet.

The first pair of thoracic appendages are *maxillipeds* (Fig. 117, D), agreeing with those of the Cumacea and Isopoda in having coupling-hooks on the endite of the basipodite. The epipodite (*ep*) projecting backwards into the branchial chamber is most fully developed in the Apseudidae, where it consists of a peduncle bearing a spoon-shaped membranous plate which terminates posteriorly in a filiform process and is produced anteriorly as a rounded lappet fringed with setae. The resemblance of this apparatus to the branchial epipodite of the Cumacea is unmistakable, and the filiform termination may be compared with the inflected apex generally found in that group. A small lobule found in some Tanaidae may perhaps represent the exopodite. In the Tanaidae the maxillipeds

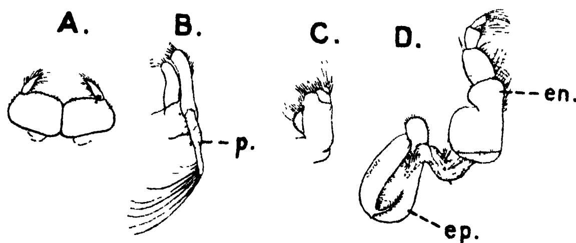


FIG. 117.

Mouth-parts of *Apseudes spinosus*. A, lower lip with movable lobes. B, maxillula; *p*, palp. C, maxilla. D, maxilliped; *en*, terminal lobe or endite of basipodite; *ep*, epipodite. (After Sars.)

are more or less united at the base, the coxopodites, and sometimes also (as in the Amphipoda) the basipodites, being coalesced.

The second pair of thoracic limbs are in nearly all cases completely chelate and are usually much stronger than the succeeding pairs. The third pair in the Apseudidae are flattened and apparently fossorial in function. The minute exopodites (Fig. 116, *ex*) with which these two pairs are provided in many Apseudidae are placed close to the exhalent and inhalent openings of the branchial cavity respectively, and by their vibratory motion assist in producing the respiratory current. In all the thoracic limbs the coxopodite is very small, and in the posterior five or six pairs the limb ends in a curved claw.

In the Apseudidae there are five pairs of *oostegites* (the first pair very small) attached to the thoracic limbs, from the second to the sixth pair. In some, perhaps all, Tanaidae only one pair of oostegites is present, on the sixth thoracic limbs.

The *pleopods* may be fully developed in both sexes, but sometimes they are reduced in number or altogether absent in the

female. The *uropods* are nearly terminal on the last segment of the body. In *Apseudes* the two rami are long, multiarticulate, and flagelliform. In other cases the rami may be much reduced and the exopodite is sometimes wanting.

Internal Anatomy.—In *Apseudes*, the alimentary canal has three pairs of *hepatic caeca*. The *heart* is elongated, extending through the six free somites of the thorax, giving off a median aortic vessel anteriorly and a pair of diverging abdominal arteries (but no median vessel) posteriorly. In *Leptochelia* and in the young of *Apseudes* it has two pairs of ostia, but in the adult *Apseudes* the right anterior ostium disappears and those of the posterior pair become asymmetrically placed. In *Tanais* only one pair persists. The anterior aorta, after dividing to encircle the brain in the median plane, forms a circumoesophageal ring, but there is no subneural sternal artery. The lateral folds of the carapace are traversed by a network of blood-channels supplied by branches from the anterior aorta, and no doubt form the chief organs of respiration, possibly assisted by the epipodites of the maxillipeds.

Considerable importance has been attached to the thoracic position of the heart in the Tanaidacea as differentiating them from the Isopoda and indicating affinity with the Amphipoda. As a matter of fact, however, in certain Isopoda (*Jaera*) the anterior end of the heart extends as far forward as it does in *Apseudes*, and the suppression of the abdominal portion, leaving intact the paired abdominal arteries, would produce a disposition of parts essentially similar to that of the Tanaidacea.

The *maxillary gland* is well developed in *Apseudes*, and a vestige of the antennal gland has been described. *Dermal glands* are commonly found on the body and limbs, and in some Tanaidae the secretion appears to be utilised in forming the tubes of mud in which the animals live. In *Heterotanais* groups of gland-cells are described situated on each side of the anterior thoracic somites and opening by long ducts on the terminal segments of the corresponding legs, an arrangement which recalls that found in certain Amphipoda. The *nerve-chain* in *Apseudes* has all the ganglia of the post-oral somites distinct.

It was stated by F. Müller that a species of *Tanais* possessed an open statocyst-cavity containing a statolith in the basal segment of the antennule, but the observation has not been confirmed.

The reproductive organs of both sexes are of a simple type. The vasa deferentia, in *Apseudes*, open close together on a median process of the last thoracic sternum. A seminal vesicle is formed in *Tanais* and in *Leptochelia* by fusion of the two vasa deferentia, but here also the external opening is paired.

Sexual differences are often strongly marked. The olfactory filaments of antennules and antennae are, as usual, more numerous

in the male; the chelae are often much stronger and differently shaped; and the pleopods are always well developed in that sex even when they are reduced or absent in the female. In several genera of Tanaidae the oral appendages, with the exception of the maxillipeds, are entirely lost by the sexually mature male. Fritz Müller described a remarkable dimorphism of the males in a species of *Leptòchelia.* One form of male was distinguished by the great development of the olfactory filaments on the antennules, and had chelae very similar to those of the female. In the other form the olfactory filaments were less numerous, but the chelae were greatly elongated and slender. These observations have been doubted by subsequent writers, but they have recently received partial confirmation from the work of G. Smith.

Development.—The embryo shows at first a dorsal curvature as in the Isopoda. A paired "dorsal organ" is present. The larvae leave the brood-pouch with the last pair of thoracic limbs and the pleopods undeveloped. In *Apseudes*, according to Claus, the lateral plates of the carapace are at first extended as wing-like processes, becoming afterwards bent downwards over the branchial epipodites of the maxillipeds and fixed in position by peg-like outgrowths of the sternum on each side.

Remarks on Habits, etc.

The Tanaidacea are exclusively marine and occur from between tide-marks to depths of over 2000 fathoms. Many burrow in mud, some inhabit tubes of mud agglutinated by the secretion of the dermal glands, and several species of Tanaidae are recorded as living in rock-crevices among a felt-like mass of filaments, presumably also secreted by the animals.

Most Tanaidacea are minute. Many species do not much exceed one millimetre in length, but some Apseudidae reach 13 mm. or more.

No fossil Tanaidacea are known.

Affinities and Classification.

Mention has been made above of the very varied opinions which have been held regarding the systematic position of the members of this order. Among recent writers, however, there is general agreement that the Tanaidacea must either stand as a distinct order or be merged in the Isopoda as the most primitive sub-order of that group. While their resemblance to the Isopoda in general form is considerable, their marked divergence in such characters as the possession of a distinct carapace, with its branchial chambers, and the form of the epipodites of the maxillipeds, fully justifies their separation.

The two families into which the order is divided are distinguished by many important characters, and it may prove necessary in the future to rank them as sub-orders.

ORDER **Tanaidacea,** Hansen (1895).

Family APSEUDIDAE. *Apseudes*, Leach ; *Sphyrapus*, Norman and Stebbing. Family TANAIDAE. *Tanais*, Audouin and Milne-Edwards ; *Heterotanais*, G. O. Sars ; *Leptochelia*, Dana.

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3. *Dohrn, A.* Untersuchungen uber Bau und Entwicklung der Arthropoden : 7. Zur Kenntniss vom Bau und der Entwicklung von *Tanais*. Jenaische Zeitschr. v. pp. 293-306, pls. xi. and xii., 1870.
4. *Sars, G. O.* Revision af Gruppen Isopoda chelifera, med charakteristik of nye herhen horende Arter og Slaegter. Arch. Math. Naturvid. vii. pp. 1-54, 1882.
5. —— Nye Bidrag til Kundskaben om Middelhavets Invertebratfauna : III. Middelhavets Saxisopoder (Isopoda chelifera). Arch. Math. Naturvid. xi. pp. 263-368, 15 pls., 1886.
6. *Smith, G.* High and Low Dimorphism : with an account of certain Tanaidae of the Bay of Naples. Mitth. zool. Stat. Neapel, xvii. pp. 312-340, pls. xx.-xxi., 1905.

Many of the works quoted in the list at the end of the next chapter deal, in part, with the Tanaidacea. See especially those of Beddard, Delage, Hansen (Plankton Expedition), Norman and Stebbing, Richardson, Sars, and Spence Bate and Westwood.

CHAPTER XII

THE ISOPODA

Order **Isopoda**, Latreille (1817).

Sub-Order 1. **Asellota.**
,, 2. **Phreatoicidea.**
,, 3. **Flabellifera.**
,, 4. **Valvifera.**
,, 5. **Oniscoidea.**
,, 6. **Epicaridea.**

Definition.—Peracarida in which there is no distinct carapace, but the first thoracic somite (rarely also the second) is coalesced with the head; the telson is rarely defined from the last somite; eyes sessile or set on immovable processes of the head; antennules uniramous (except in *Bathynomus*); antennae sometimes with a minute exopodite; thoracic limbs without exopodites; first pair modified as maxillipeds, the epipodite, when present, not enclosed in a branchial cavity; remaining pairs all similar or variously modified, coxopodite always short, often fused with the body and expanded laterally; pleopods typically biramous, with lamellar, branchial rami, generally the second and sometimes also the first ·r modified in the male; heart lying wholly or partly in abdomen; ··oung leave the brood-pouch before the appearance of the last ·horacic limbs.

·*al.*—The terrestrial habits of the more familiar members and the close resemblance which some of them bear to ·a (Oniscomorpha), led to their being widely separated ·ustacea in many of the earlier systems of classifi- ·le, to whom the name Isopoda is due, placed · Insecta. Leach ranked them along with ·oup Edriophthalma, thus giving them the · in most modern systems. Our know- ·lassification of the Isopoda is largely ·ian naturalists, especially to the G. O. Sars, Bovallius, Budde-

Lund, and Hansen. The remarkable group of the Epicaridea has attracted many investigators, but it is especially to the memoirs of Giard and Bonnier that the student must turn for a clear account of their structure and complicated life-histories. As regards the internal anatomy of the Isopoda, the literature is scattered and fragmentary, but Delage's study of the circulatory system must not be passed without mention. Bullar's discovery of hermaphroditism among the Cymothoidae is also noteworthy.

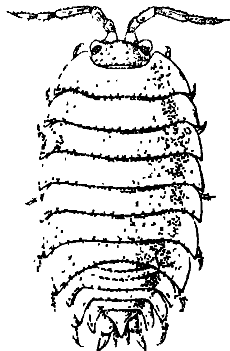


Fig. 118.
Porcellio scaber, ♀, dorsal view. × 3. (After Sars.)

Morphology.

In the majority of the free-living Isopoda the body (Fig. 118) is more or less flattened, with an oval outline as seen from above and with a short abdominal region. In the Arcturidae and Anthuridae, however, it is elongated and subcylindrical, and in some of the latter family it is almost vermiform. In *Phreatoicus* (Fig. 119) the body is laterally compressed and the aspect is that of an Amphipod. In the parasitic Epicaridea the adult female

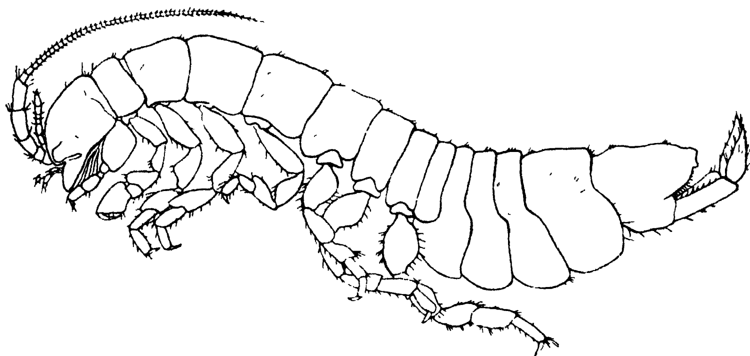


Fig. 119.
Phreatoicus assimilis, ♀, from the side. × 8. (After Chilton.)

becomes more or less distorted and deformed and may even lose all trace of segmentation. In addition to the first, the second thoracic somite becomes united with the head in the Gnathiidae and Serolidae, in the genus *Stenasellus* among the Asellota, and a few Valvifera. The last thoracic somite occasionally remains of small size and without appendages in the adult, as it nearly always is in the

young. Very often some or all of the abdominal somites are fused together, and the last somite is always coalesced with the telson except in certain Anthuridae. The abbreviation of the abdomen is least in the Phreatoicidae; in the other families the anterior somites are short and crowded together, though the telsonic segment is often of large size. The abdominal somites are usually expanded laterally into pleural plates, and the thoracic somites may be similarly produced over the bases of the legs, but in these the pleural plates are often supplemented or replaced by the expanded coxopodites which here form the *coxal plates* or so-called "epimera."

Appendages.—The *antennules* are usually short, and in the Oniscoidea they are almost or quite vestigial. They are never biramous except in *Bathynomus*, where a minute vestige of the inner flagellum is present, and in the cryptoniscan larvae of some Epicaridea.

The *antennae* vary much in length, being several times as long as the body in some Asellota, while in the Epicaridea they are hardly more than vestiges. The peduncle usually consists of five segments, but in the Asellota and in *Bathynomus* and *Cirolana* it has six. In the Asellota a minute movably articulated scale representing the exopodite is sometimes present on the third segment. In all other Isopoda the exopodite is absent. In the Arcturidae the antennae are very large and strong and are used in seizing prey.

The mouth-parts of the Isopoda show great diversity of structure, many modifications being correlated with the parasitic or semi-parasitic habits of certain groups. In the more typical forms (*e.g. Asellus*) the *mandible* carries a palp of three segments, and has a serrated incisor process, with a lacinia mobilis, at least on the left side of the body, a row of spines, and a strong molar process. The molar process is movably articulated with the body of the mandible in the Cirolaninae (Fig. 120, A). The *maxillula* (Fig. 120, B) has two endites (corresponding, according to Hansen, to the first and third segments) directed distally and bearing strong setae or spines. There is no trace of a palp such as exists in the Tanaidacea. The *maxilla* (Fig. 120, C) has three endites, the proximal one directly continuous with the basal part and directed obliquely inwards; the two others are directed distally, overlapping each other and movably articulated with the basal part; Hansen regards these as resulting from the division of a single endite corresponding to the third segment.

The first thoracic limb is always specialised as a *maxilliped* (Fig. 120, D) and closely associated with the other mouth-parts. It has a short but distinct coxopodite bearing externally a lamellar epipodite (*ep*) generally more or less indurated, and not, apparently, branchial in function as it is in the Tanaidacea, but serving as an

operculum to cover the lateral parts of the other oral appendages. The basipodite is produced distally into a large endite (l^2) which is sometimes movably articulated (*Bathynomus*, *Cirolana*, *Chiridotea*), and which bears one or more coupling-hooks (*c*) interlocking with those of the opposite side. The endopodite or palp consists, in the typical case, of five more or less lamellar segments, but the number is often reduced. In the ovigerous females of *Asellus* and of certain genera of Valvifera the coxopodite bears a small lappet, fringed with setae, projecting backwards into the marsupium and

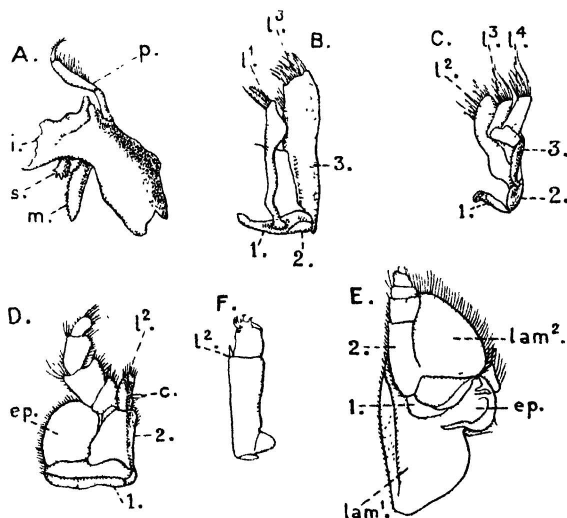


FIG. 120.

Mouth-parts of various Isopoda. A, mandible of *Cirolana borealis*. B, maxillula of *Chiridotea entomon*. C, maxilla of same. D, maxilliped of same. E, maxilliped of adult female of *Rocinela danmoniensis*. F, maxilliped of adult male of same. *c*, coupling-spine; *ep*, epipodite; *i*, incisor process; l^1, l^2, l^3, l^4, endites of successive segments of the appendages (according to Hansen's later interpretation the endites l^3, l^4 of the maxillula result from the division of a single endite); *lam*$^{1-2}$, laminar outgrowths of first and second segments of maxilliped; *m*, molar process; *p*, palp; *s*, lacinia mobilis and spine-row of mandible, which in this case are closely associated together; 1, 2, 3, successive segments of the appendages. (After Hansen.)

resembling the coxal appendage of the second thoracic limb in the females of Cumacea. A similar plate, more largely developed, is found in the females of Cymothoidae (Fig. 120, E) and Epicaridea and of some genera of Sphaeromidae, where it is associated with an expansion of the basipodite and with the epipodite, giving a lamellar character to the whole appendage. In all these cases the vibratory motions of the maxilliped cause a current of water to pass through the marsupium for the aeration of the developing embryos. A similar expansion of the basipodite united with the epipodite occurs also in *Serolis*, where, however, the coxal lobe is not developed. The position of this coxal lobe and its occurrence

only in the adult female suggest its possible homology with the oostegites of the following somites.

As an example of extreme modification of the mouth-parts and of exceptionally marked changes taking place during development,

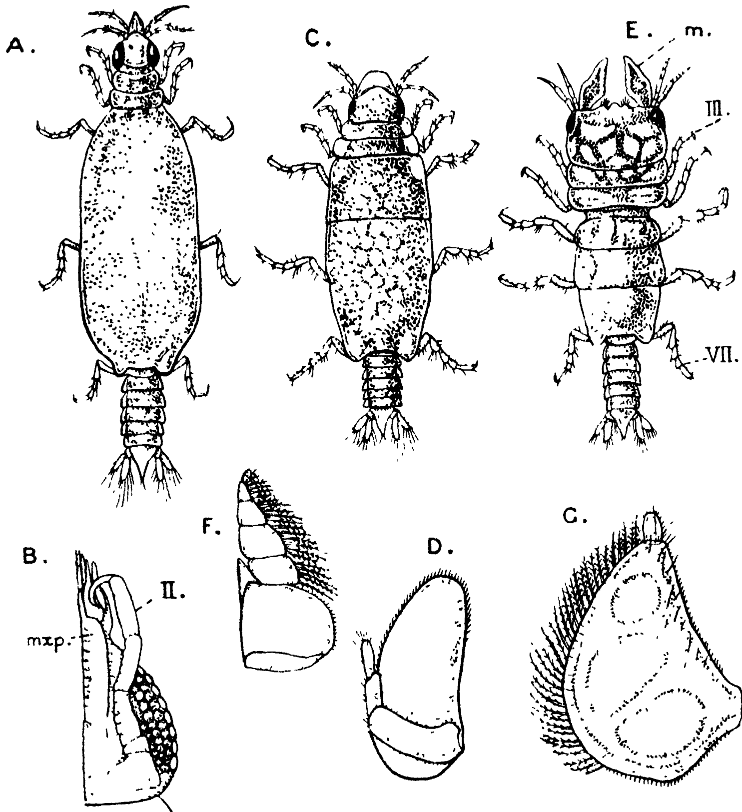


Fig. 121.

Gnathia maxillaris. A, late larval form (Praniza-stage). B, head of same, from below, further enlarged. C, adult female. D, second thoracic appendage of same, further enlarged. E, adult male. F, maxilliped (first thoracic appendage) of same, further enlarged. G, second thoracic appendage of same. *m*, mandible of male; *mxp*, maxilliped of larva; II, III, VII, second, third, and seventh thoracic appendages (the eighth is undeveloped in adults of this family). (After Sars; B partly after G. Smith.)

the oral apparatus of the very aberrant *Gnathia* may be here described. In the larval state (Fig. 121, A), *Gnathia* is parasitic on fish, and the suctorial mouth-parts form a short conical proboscis (Fig. 121, B). The mandibles are styliform, finely serrate on the inner edge, without palp, molar process, lacinia mobilis, or spines. The maxillulae and maxillae are simple, slender

styles. The maxillipeds (*mxp*), which close the oral cone below, have an elongated basipodite produced distally into a slender endite, with many coupling-hooks; the next segment is also produced distally as an acute, serrate point, and the remaining segments of the endopodite are coalesced into a short palp. The appendages of the second thoracic segment (II), which in this family is coalesced with the head, lie on either side of the oral cone and end in strong curved claws which no doubt assist in penetrating the skin of the host. The adult animals are free-living and have the mouth-parts very differently developed in the two sexes. In the male (Fig. 121, E) a pair of relatively enormous mandibles (*m*) are articulated at the outer corners of the front margin of the head and are apparently used only as defensive weapons. The small aperture of the mouth is placed much further back on the lower surface of the head. The maxillulae and maxillae are entirely lost. The maxillipeds (Fig. 121, F) are broad and flattened, composed of six segments tapering gradually to the apex; the endite of the basipodite is small and the other segments are fringed externally with long plumose hairs. The appendages of the second segment (Fig. 121, G) have lost the pediform character which they have in the larva and in all other Isopoda, and form a pair of overlapping valves closing over the oral area. Each consists of a large oval plate showing traces of three segments and bearing distally one or two minute terminal segments. In feeding, these valves are opened out and the vibratory movements of the maxillipeds produce a current of water which is supposed to carry food-particles towards the mouth. In the female (Fig. 121, C) the mandibles have disappeared and the maxillipeds are similar to but smaller than those of the male. The second thoracic limbs (Fig. 121, D) are, however, very different, consisting of a small leg-like appendage of three segments, having at its base a large oval plate which probably represents an oostegite, although, in this genus, distinct oostegites are not found on any of the other limbs.

In the Epicaridea the styliform mandibles are enclosed in a suctorial "oral cone" formed by the upper and lower lips. The maxillulae and maxillae are vestigial or absent, and the lamellar maxillipeds serve, as already mentioned, to keep a current of water flowing through the brood-pouch. In the ovigerous females of many Cymothoidae the mouth-parts are covered by the anterior oostegites, so that the animal is incapable of feeding, and in some genera of Sphaeromidae the mouth-parts of the adult females (with the exception of the maxillipeds) are reduced and functionless.

The last seven pairs of thoracic appendages in the Isopoda are typically developed as walking-legs which may, as in the Oniscoidea, present a uniformity of size and shape justifying the name Isopoda,

but which in other cases undergo many modifications for prehensile, natatory, and other functions. The coxopodite has the form of a complete segment movably articulated with the body only in the Asellota (Fig. 122, *cx*). In all other Isopoda it is more or less completely fused with the body and is often expanded into a *coxal plate* overhanging the attachment of the limb and replacing the pleural expansion of the somite to which it belongs. An interesting series illustrating this substitution can be traced within the family Idoteidae. In *Idotea hectica* (Fig. 123, A), the pleural plates (*pl*) of the thoracic somites are well developed and completely cover the coxopodites (*cx*), of which the outline can be traced on the

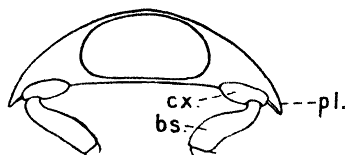


FIG. 122.

Thoracic somite of *Jaera marina*, separated and seen from in front. *bs*, basipodite of thoracic leg; *cx*, coxopodite; *pl*, pleural plate.

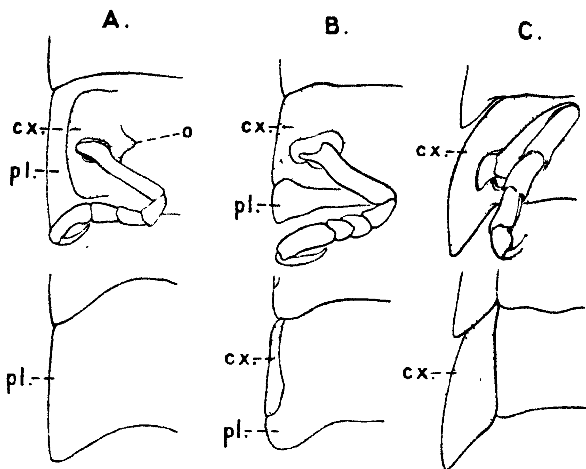


FIG. 123.

Margin of thoracic somites of, A, *Idotea hectica*; B, *I. ochotensis*; C, *Chiridotea sabini*. The upper figures show the under surface, the lower the upper surface. *cx*, coxal plate (dotted); *pl*, pleural plate; *o*, rudiment of oostegite.

under-side of the plates near the outer edge. In other species of the same genus (Fig. 123, B) the coxal plate projects beyond the outer margin of the pleuron for a part of its length so as to be visible on the upper surface. In yet other species of the genus and in the allied *Chiridotea* (Fig. 123, C), the pleura are no longer to be distinguished, and their place is taken by the greatly developed coxal plates, which are marked off, on the dorsal surface, by distinct sutures, generally allowing a slight amount of move-

ment. This condition is found in the Cymothoidae, Serolidae, some Sphaeromidae, and in the Tylidae among the Oniscoidea. When the suture line disappears, as in most Oniscoidea (Fig. 118), it is impossible to distinguish the coxal plate from a true pleuron. In all Isopoda, however, with the single exception of the genus *Plakarthrium* (Sphaeromidae), the coxopodites of the second thoracic somite (the first free somite) are completely coalesced with the body.

The ischiopodite of the thoracic legs is generally more or less elongated, not very short as it is in Tanaidacea and Amphipoda. The dactylopodite generally ends in a stout claw which may be completely coalesced with the segment or defined from it by a suture. In *Janira* and some other Asellota, however, there are several stout claw-like spines.

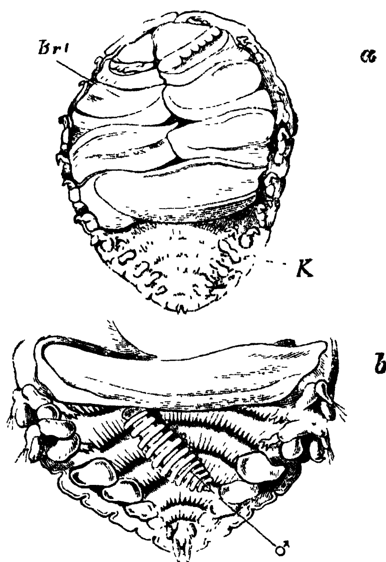


Fig. 124

Gyge branchialis (Bopyridae). *a*, female, seen from ventral side; *Brl*, oostegite; *K*, abdominal appendages. *b*, abdomen of same with adhering male (♂), further enlarged. (After Cornalia and Panceri, from Claus's *Textbook*.)

Very commonly one or more of the anterior pairs of thoracic legs assume a prehensile function and become more or less completely subchelate, through never forming a perfect chela such as is found among the Tanaidacea. The most perfect natatory legs are found in *Munnopsis* and related genera, where the last three pairs have the carpus and propodus expanded into oval paddles fringed with long setae.

In *Amesopous* (Valvifera) the fourth and fifth pairs of thoracic appendages (first and second peraeopods) are unrepresented, except by the oostegites in the female, a condition curiously repeating that found in the Caprellidea among Amphipoda.

The *oostegites* (Fig. 124, *Brl*), which, in the great majority of Isopoda as in other Peracarida, form the brood-chamber of the female, are clearly seen in the Asellota to be attached to the coxopodites of certain of the thoracic legs. In the other tribes the coxopodites are more or less completely coalesced with the corresponding somites and the oostegites appear to spring from the ventral surface of the body close to the bases of the legs. In certain Cymothoidae and Epicaridea a pair of oostegites is present

on each of the seven free thoracic somites, the last two pairs, however, being very small. If, as has been suggested above, the coxal lobe of the maxillipeds is homologous with the oostegites, we have the possibility of these structures being developed on all the thoracic appendages. More usually, however, only the first five free somites bear oostegites, and the number may be still further reduced, certain genera of Arcturidae possessing only one pair attached to the fourth free somite.

Though the development of the oostegites has been traced in only a few cases, it is known that important differences occur in this respect. In *Asellus* they appear as small buds from the coxopodites, increasing in size at successive moults until maturity is reached. In the Oniscoidea, on the other hand, no trace of oostegites is visible externally up to the moult which immediately precedes oviposition. Just before this moult they are developed underneath the cuticle, and when this is cast off they at once expand to their full size. Special structures aiding or replacing the oostegites in containing the brood will be described later in connection with the reproductive system, but it may be noted here that in a few Isopoda (*Cassidina* and a few allied genera among the Sphaeromidae, and some Epicaridea) the oostegites appear to be entirely wanting.

The *pleopods* are almost always biramous, with a short protopodite in which three segments can be recognised in *Bathynomus*, and with lamellar rami generally overlapping each other with the exopodite in front. One or both of the rami may be crossed by a suture-line dividing it into two segments. In the simpler cases all the pleopods are similar (except for the sexual modifications to be described below), both rami serving as respiratory and in many cases also as natatory organs. The latter function is indicated by a marginal fringe of long setae and by the presence of a group of coupling-hooks on the inner side of the peduncle. Pleopoda of this type are found with comparatively slight modifications in the Phreatoicidae, Gnathiidae, and Cymothoidae, but in some members of the last two families the natatory setae, present in the young, are lost in the adult. This is the case also in the Epicaridea, where the pleopoda of the adult may become much reduced or altogether suppressed, or may, on the other hand, develop into arborescent branchiae. In the aberrant Cymothoid *Bathynomus* the endopodites bear tufts of ramified branchial filaments. Even in the Cymothoidae, however, the uniformity of the pleopods is slightly qualified by the fact that the endopodite of the fifth pair is always devoid of marginal setae. This leads to the specialisation of functions found in Sphaeromidae and Serolidae, where the anterior pairs (the first three in Serolidae and many Sphaeromidae) are exclusively natatory and the posterior pairs exclusively branchial.

In many Sphaeromidae one or both rami of the last two pairs are transversely plicated so as to increase the respiratory surface. In some members of these families the exopodite of the fifth pair is more or less indurated and forms a kind of operculum protecting the more delicate appendages behind it. Opercular structures having a similar function are formed in different ways in other families. In some Anthuridae the first pair of pleopods are enlarged and cover the remaining pairs. In the Asellidae and Stenetriidae the exopodite of the third pair performs the same function. In the Parasellidae an unpaired plate formed by the coalescence of the first pair forms the operculum in the female, the male having a tripartite operculum formed by the first and second pairs. In the Valvifera (Fig. 125), finally, the pleopods are covered in by the valve-like uropods. A very special line of modification has been followed in the case of the Oniscoidea. In the Ligiidae, which are in many ways the most primitive family, the pleopods are all similar, with the exopodites stouter than the endopodites but sharing in the respiratory function. In many genera of the remaining families, however, the exopodites of the first and second, and sometimes of all five, pairs are specially adapted for aerial respiration by the development within them of small cavities opening to the exterior by slit-like apertures and giving rise internally to a system of ramifying tubules filled with air (Fig. 126). These tubules, which are lined with a delicate chitinous cuticle, are known as *pseudo-tracheae* (*tr*). In certain cases (*Oniscus*) in which pseudo-tracheae are absent, their place is taken by a system of air-filled spaces immediately under the cuticle of the exopodite. These spaces do not communicate with the exterior, and appear to become filled with air by diffusion through the cuticle.

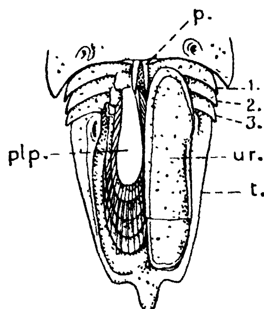


FIG. 125.

Under-side of abdomen of male *Idotea baltica*, with one of the uropods removed to show the pleopods. 1, 2, 3, first three somites of abdomen; *t*, telsonic segment comprising the last three abdominal somites coalesced with the telson; *plp*, pleopods; *ur*, uropod; *p*, penes, attached to sternum of last thoracic somite. (After Sars.)

In the majority of Isopoda the second, and sometimes also the first, pair of pleopods present special modifications in the male sex, the only exceptions being the Epicaridea and the small and aberrant family of the Gnathiidae, among the Flabellifera, where no such modification is found. In the remaining families of the Flabellifera and in the Phreatoicidea and Valvifera, the lamellar endopodite of the second pair bears, in the male sex, a rod-like process (*appendix masculina*) (Fig. 127, *m*) articulated with its inner

edge and grooved for the reception of the bundles of spermatozoa which it is its function to transfer to the female. This rod appears

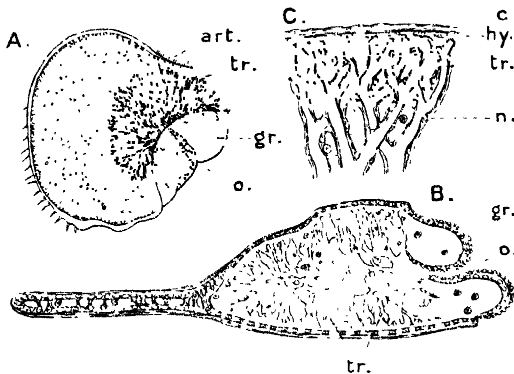


FIG. 126.

A, exopodite of first pleopod of *Porcellio scaber*; the tuft of pseudo-tracheae is seen through the transparent cuticle. B, vertical transverse section through same. C, part of section further enlarged. *art*, point of articulation of exopodite with peduncle; *c*, cuticle; *gr*, "grooved area" of cuticle; *hy*, hypodermis; *n*, nucleus of hypodermis of pseudo-tracheal tube; *o*, external opening of pseudo-tracheae; *tr*, pseudo-tracheae. (After Stoller.)

to be the distal segment of the endopodite. In the groups just mentioned the pleopods of the first pair are similar or present but slight differences in the two sexes, but in the majority of the Oniscoidea and in the Asellota the first pair are also modified in the male sex. In the males of the Oniscoidea the inner ramus of the second pair is styliform and composed of two segments, of which the proximal corresponds to the main part of the endopodite in groups above mentioned. In the family Ligiidae this is the only modification of the pleopods in the male sex, but in all the other Oniscoidea the first pair have the endopodites also styliform, though unsegmented.

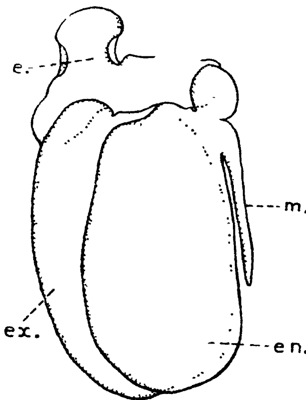


FIG. 127.

Second pleopod of an ovigerous female of *Nerocila maculata*, showing persistence of the appendix masculina (*m*). *en*, endopodite; *ex*, exopodite; *e*, laminar expansion from outer edge of protopodite.

In the Asellota the sexual modifications of the pleopods are more complex and differ from those of all other Isopoda. The second pair are always absent in the female. In the females of Asellidae the first pair are small, uniramous, and separate; in the Stenetriidae and Parasellidae they are coalesced,

forming, in the latter family, a large operculum which completely covers the following pairs. In the male sex the Asellidae have the first pair not greatly different from those of the female; the second pair are small, with a short protopodite and two rami, each of two segments, the endopodite having a cavity in the distal segment. In the Stenetriidae the first pair are partly fused together and the second pair are to some extent intermediate in structure between those of the other two families. In the Parasellidae the first pair are fused together, their enlarged protopodites each with a small immovable terminal ramus forming the middle plate of a tripartite operculum, of which the lateral parts are the enlarged protopodites of the second pair. The rami of the latter pair are borne on the inner margin of the protopodite; the exopodite of two segments is hook-shaped and serves to fasten the lateral to the middle plate of the operculum; the endopodite forms a geniculate copulatory organ of two, sometimes of three segments, with a cavity in its distal part communicating with the exterior by a narrow canal.

In most Isopoda the *uropods* differ widely in form and position from the pleopods. In the adult females of some Epicaridea, however, the uropods do not differ, except in size, from the appendages in front of them, and this is also the case in the Cymothoid genera *Anuropus* and *Branchuropus*, where they resemble the pleopods in structure and position and appear to share their branchial function. Although the uropods are usually biramous, one or other of the rami may disappear in many Asellota, some Sphaeromidae, Valvifera, and Oniscoidea. The uropods are entirely wanting in the Sphaeromid *Vireia* and in some Epicaridea. The rami are never composed of more than one segment except in the Asellotan *Acanthocope*, where the uniramous uropods present three or five segments, including the peduncle. In the Valvifera the uropods are curiously modified in form and position (Fig. 125). They are attached far forwards at the sides of the greatly enlarged telsonic segment, and are folded inwards so as to cover completely the branchial pleopods. Each consists of a large plate formed by the expanded protopodite with the small endopodite at its tip, while the exopodite [1] is vestigial or absent. In many Anthuridae the exopodite is attached near the base and the endopodite at the tip of the elongated peduncle (leading to the erroneous statement that the endopodite has two segments), and the exopodite is usually folded backwards over the dorsal surface of the telson.

Alimentary System.—The stomodaeum forms, in the majority of Isopoda, a masticatory stomach, which is comparatively simple in

[1] What is here called the exopodite is usually regarded as the endopodite, and *vice versa*. The interpretation given above depends on the assumption that the uropods have reached their present position by a movement of *rotation*, not of simple translation.

Asellus and *Chiridotea* and more complicated in the Oniscoidea. The number of types in which its structure has been studied is, however, too small to admit of profitable comparisons between them. In parasitic forms with suctorial mouth-parts the fore-gut is probably always more or less modified, but little is known of the details except in some Epicaridea. In the Entoniscidae the short and narrow oesophagus leads into a spherical or bilobed chamber, the cephalogaster, lined with villi and rhythmically contractile. This is followed by a second chamber, of which the lumen is reduced to a crescentic section by a strong ridge or typhlosole on the dorsal side clothed with setae which constitute an effective strainer. A third chamber with muscular walls, contracting alternately with the cephalogaster, is known as Rathke's organ. In the Bopyridae the cephalogaster alone has been recognised.

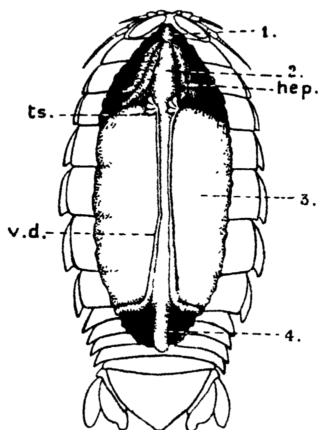


FIG. 128.

Aega psora, ♂, dissected from the dorsal side to show the alimentary and reproductive systems. 1, stomodaeal region of the alimentary canal; 2, thick-walled, suctorial part; 3, thin-walled reservoir; 4, intestine; *hep*, hepatic caeca; *ts*, testis; *v.d*, vas deferens.

Three pairs of hepatic caeca are present in Idoteidae and Cymothoidae (Fig. 128, *hep*); two pairs in *Asellus*, *Serolis*, and the Oniscoidea (except *Ligia*, which has three); and only one pair in *Gnathia*, *Paranthura*, and the Epicaridea, in which group the caeca may give off diverticula. It has been stated that, apart from the hepatic caeca, the mid-gut of the embryo gives rise to only a very short region of the alimentary canal; but this has been disputed, and it seems not unlikely that considerable differences may exist in this respect between the members of the order. In the blood-sucking *Aega* (Fig. 128) the stomodaeum (1) is very short, so that the point of attachment of the hepatic caeca is near the anterior end of the gut. It is followed by a thick-walled part (2) which may possibly have a suctorial function. At about the fourth thoracic somite this suddenly dilates into a thin-walled chamber (3) of relatively enormous size, completely filling and distending the posterior thoracic somites when filled with blood. If this reservoir be really of proctodaeal origin it seems difficult to suppose that it does not exercise an absorptive function.

In some Epicaridea (Entoniscidae, *Hemioniscus*) the proctodaeal invagination fails to unite with the anterior part of the gut and either ends blindly or disappears altogether in the adult.

Circulatory System.—The most striking features of the circulatory

system in the Isopoda are the great development and minute ramification of the arterial vessels in the more specialised types and the posterior situation of the heart, the latter feature being correlated with the localisation of respiration in the abdominal appendages.

The heart lies at the junction of thorax and abdomen, extending for varying distances into each. When elongated and tubular it may lie for the greater part of its length in the thorax (*Jaera*) or be produced backwards into the abdomen. When shortened and saccular it lies mainly in the abdomen, only extending into the last thoracic somite. It communicates with the well-defined pericardium by one or two pairs of ostia.

Anteriorly the heart gives off the median aorta and seven pairs of lateral thoracic arteries. Of these the three posterior usually originate separately from the heart, the remaining four arising from a common trunk on each side. Rarely all seven pairs spring laterally from the aorta. Anteriorly the aorta passes behind and below the brain to form, except in certain degraded or parasitic forms, an oesophageal ring encircling the gullet in front of or below the oesophageal nerve-ring. Posteriorly this ring is connected with a ventral system of vessels which vary considerably in their arrangement. In the more typical cases (Cymothoidae, Sphaeromidae) a large median *subneural* artery runs backwards from the oesophageal ring along the sternal surface of thorax and abdomen, giving off numerous lateral branches. The lateral thoracic arteries mentioned above also contribute to the ventral system, each one bifurcating as it reaches the lateral part of the corresponding somite, one branch passing into the limb and the other ramifying towards the middle line. Between the ultimate ramifications of these two sets of vessels, those, namely, of the subneural and of the ventro-lateral arteries respectively, anastomoses frequently occur, and in this way a communication is established in each somite between the dorsal and the ventral arterial systems. But, in addition, in one or other of the thoracic somites it is found that the ventro-lateral artery on each side passes directly into the subneural vessel, thus establishing a complete arterial circle. In certain forms (*Idotea*, *Ligia*) the subneural artery is for the most part absent, and the ventral system is formed almost entirely by the ramifications of the ventro-lateral arteries. Vestiges of the subneural artery, however, persist anteriorly where a short trunk runs backwards for a little way from the oesophageal ring, and posteriorly where an abdominal trunk is formed by anastomosis of branches from the last pair of ventro-lateral arteries, while in the thorax similar anastomoses give rise to a succession of short vessels in the middle line as though the subneural vessel had become disintegrated into sections.

The posterior end of the heart always ends blindly and is never

continued into a posterior median aorta. In place of this, however, a pair of abdominal arteries (which may unite into one immediately after their origin), springing from the ventral surface of the heart (or, exceptionally, from the last pair of thoracic arteries), run backwards and send off numerous branches. In certain forms with natatory pleopods (*Conilera*) where the muscles of the abdomen are greatly developed, these vascular ramifications attain a remarkable degree of complexity. The minute subdivision of the ultimate arterial branches is also well shown by the vessels supplying the hepatic caeca.

From the lacunae of the haemocoel the blood is carried to the branchial pleopods by sinuses which vary somewhat in their arrangement in the different types. A median ventral abdominal sinus is nearly always present from which afferent branchial vessels are given off. Sometimes there are also two great sinuses running along the lateral margins of the thorax. From the pleopods the blood is returned by efferent branchial vessels to the pericardium. In addition to the arterial blood thus received, it appears that a small amount of venous blood may also enter the pericardium by some small apertures in its anterior part communicating with the general lacunar system of the body. The existence of these apertures is important as a starting-point for comparison with the very different circulatory system of the Amphipoda.

Excretory System.—The antennal gland of the Isopoda, unlike that of the Amphipoda, appears to persist only in a vestigial condition. In *Asellus* and some Oniscoidea it has been recognised as a small vesicle or a solid mass of cells without communication with the exterior. A well-developed maxillary gland of the usual type has been found in *Asellus*, and in *Ligidium* and some other Oniscoidea. In the Oniscidae it is reduced in size, and appears in some cases to have no external opening. It has been suggested that in some of the terrestrial species it may have a salivary function.

It seems probable that in many Isopoda the excretory products are got rid of by being stored in the so-called "fat-bodies." An excretory function has also been attributed to certain glands opening on the ventral surface of the posterior thoracic and abdominal somites.

Nervous System.—The ventral nerve-chain presents various degrees of concentration and coalescence of the ganglia, not always in correspondence with the degree of fusion of the somites. In *Chiridotea* and *Sphaeroma* seventeen distinct ganglia are found, corresponding to all the post-oral appendages, and in *Sphaeroma* an additional ganglion is found in the telson which is not represented in any other Eumalacostracan. In most cases, however, the ganglia in front of the second thoracic form a single mass, and not more than four ganglia are generally distinct in the abdomen.

Sense-Organs.—In *Munna* and some allied Asellota the eyes are set on prominent lateral lobes of the head, but there is no evidence that these represent the movable ocular peduncles of the primitive Malacostraca. The number of ommatidia in each eye varies from four in *Asellus* to about 3000 in *Bathynomus*. The crystalline body is generally bipartite, but in one of the ommatidia in each eye of *Asellus* it is tripartite. The number of retinular cells and of rhabdomeres may be 4, 5, or 7 in different genera.

The only Isopoda in which statocysts have been observed are *Anthura gracilis*,[1] and another species of Anthuridae, where they have recently been described by Thienemann. A pair of them are situated in the anterior part of the telson. Each communicates with the exterior by a fine canal and contains a single statolith. Muscles are attached to the wall of each statocyst. In view of the sluggish movements and burrowing habits of the Anthuridae, their possession of these organs is somewhat remarkable.

Reproductive System.—The ovaries vary in form, but are generally elongate and tubular and are not connected with each other in the middle line. In some Epicaridea they give off segmentally arranged diverticula. The oviducts are short and simple, occasionally (*Asellus*) dilating to form a sperm receptacle. A peculiarity which is quite unique among Crustacea is presented by certain Epicaridea (Hemioniscidae, Liriopsidae) which have *two* pairs of oviducts. As the oviducts, or at least their external apertures, are not developed until the segmentation of the body has disappeared in the adult females, it is not possible to determine whether both pairs belong to one somite.

A remarkable cycle of changes takes place in the female reproductive organs of the Oniscoidea. When sexual maturity is reached, but before the oostegites have developed, the generative apertures are present in the usual position, but instead of communicating with the oviducts, each leads into a blind invagination of the integument, which functions as a receptaculum seminis. After this has been filled with sperm in copulation, it acquires a communication with the oviduct and the sperms pass up into the ovary. At the next ecdysis the receptacula disappear and the oviducts no longer communicate with the exterior. The fertilised eggs are stated to pass into the body-cavity and from thence to the marsupium by way of a slit-like unpaired aperture between the last two thoracic somites. This statement, however, can hardly be accepted without further confirmation, as the existence of a free opening from the body-cavity (haemocoel) to the exterior would be quite unparalleled among Arthropoda. A second lot of eggs are fertilised by sperms remaining in the oviducts and pass into the marsupium after the first brood have left it. After liberation of the second brood,

[1] According to Gurney, the species is really *Cyathura carinata* (Kroyer).

ecdysis takes place, the oostegites are cast off and receptacula are again developed, the animal reverting to the condition in which it was before impregnation.

The arrangement of the oostegites which form the marsupial chamber in all normal Isopoda has already been described. In certain cases, however, brood-pouches are formed in other ways. In the section Cryptoniscina among the Epicaridea a series can be traced in which the oostegites diminish in size and finally disappear, their place being taken by lateral folds of the body. The term of the series is given by *Hemioniscus*, in which the brood-cavity is from the first completely closed, arising by delamination in a thickening of the ventral ectoderm.

A remarkably varied series of adaptations for carrying the eggs and young have recently been made known in the family Sphaeromidae. In some members of this family the marsupium is formed by the oostegites in the usual manner, but in others special brood-pouches are formed by invaginations of the ventral integument, and in some cases here also oostegites are quite wanting.

In addition to their protective function in sheltering the eggs and young, it has been suggested that the oostegites may in some cases supply nourishment to the developing embryos. In certain Oniscoidea papilliform projections from the sternal surface of the thoracic somites have also been credited with this function.

The testes, in the majority of Isopoda, consist each of three follicles (Fig. 128, *ts*) opening into a common vas deferens (*v.d*). Only in a few cases is the number of follicles reduced to one on each side. The external openings are generally set on papilliform or tubular processes (penes) (Fig. 125, *p*), which may be fused into one (Oniscoidea, except Ligiidae, Arcturidae). In the Epicaridea the penes are commonly absent and the aperture may be paired or single, but in *Priapion* a bifurcated penis of great size is present.

The position of the penes sometimes departs a little from the general rule among Malacostraca in so far as they may spring, not from the last thoracic sternum, but from the articular membrane between it and the first abdominal somite, and may even be attached to the sternum of the latter. It is very improbable, however, that the vasa deferentia ever perforate the copulatory appendages of the second pleopods as they have been stated to do in the Tylidae (Oniscoidea).

The occurrence of protandrous hermaphroditism has been demonstrated in certain genera of the sub-family Cymothoinae among the Cymothoidae, and of the tribe Cryptoniscina among the Epicaridea. It is not known to occur in the other sub-families of the Cymothoidae; and though its limits within the group Epicaridea are not exactly known, it is certain that many of the families, probably the whole of the tribe Bopyrina, are definitely

of separate sexes. In certain Cymothoinae the external characters of the male sex do not completely disappear when the individual passes into the female phase, the copulatory appendage of the second pleopods sometimes remaining of conspicuous size even in specimens which have the marsupium filled with eggs (Fig. 127). As in many other Crustacea, traces of hermaphroditism probably exist normally in the young of many Isopoda. In *Sphaeroma*, vestiges corresponding to the three testicular follicles are found at the anterior end of the ovary in young specimens, and what may be a vestige of the oviduct is found in the male.

Mention may be made here of the supposed occurrence of "hypodermic impregnation" in the Asellotan *Jaera*. It is stated that a spermatophore is inserted by the male between the thoracic terga of the female, and that it penetrates the articular membrane and passes into the body-cavity, discharging its contents into the oviduct, while the empty capsule is expelled by the oviducal aperture. The account of this extraordinary process cannot, however, be accepted without further investigation.

Development.

The eggs are usually large, with superficial segmentation. In *Hemioniscus*, however, which, from the peculiar formation of the marsupium, is practically viviparous, the eggs are minute, without yolk, and undergo complete and equal segmentation, giving rise to a hollow blastosphere. It is characteristic of the Isopoda, as contrasted with the Amphipoda, that the developing embryo is curved towards the dorsal side. A "dorsal organ" is present in many Isopod embryos, and assumes very diverse forms. In Cymothoidae it arises as a thickened plate of cells which becomes invaginated, forming a small cavity opening to the exterior by a narrow neck. In *Oniscus*, on the other hand, the thickening is stated to become constricted off from the dorsal surface and to form a saddle-shaped plate partly enveloping the embryo and connected with it only by a narrow stalk, but the accuracy of this account has been denied. In *Asellus* a pair of trilobed hollow processes grow out from the sides of the thoracic region. These have been regarded as representing the dorsal organ, but Claus has compared them with the lateral wings of the carapace in the larva of *Apseudes*. A distinct carapace-fold has been described in the embryo of *Jaera*, extending, at first, over the region of the second thoracic somite, but afterwards becoming reduced. Transitory rudiments of exopodites are stated to be present on the thoracic limbs in early embryos of *Ligia*.

In all Isopoda the young leave the brood-pouch with the last pair of thoracic limbs undeveloped (as in Tanaidacea and Cumacea), but otherwise in most free-living species the young are very similar

to the adults. In many parasites, however, a certain amount of metamorphosis occurs. In the Cymothoinae, for instance, the young are free-swimming, but the adults lose the natatory setae of the pleopods and undergo considerable changes of shape in becoming permanently attached to the host. In this case the life-history is complicated by the fact that each individual passes through stages in which it presents the characters, first of the male, and afterwards of the female sex. The remarkable changes in the structure of the mouth-parts, which are accompanied by considerable changes of general shape, in the Gnathiidae have already been described.

It is in the Epicaridea, however, that the changes during development are most profound. In spite of the great diversity of structure among the adults, the natural character of this gro ip is rendered evident by the uniformity of the larval stages throughout all the families. In the first or epicarid stage ("stade épicaridien," Bonnier) (Fig. 129, B) the body is short and broad and strongly convex dorsally, with seven thoracic and six abdominal somites distinct; the antennules are very short, the antennae longer and used in swimming, and both are sparingly provided with sensory filaments; six pairs of thoracic legs are present, all, except sometimes the posterior pairs, strongly subchelate; the pleopods are uni- or biramous, with natatory setae; the uropods are usually biramous and styliform; the telsonic segment is generally produced into an "anal tube"; eyes are usually present but imperfectly developed. In the last larval or cryptoniscan stage ("stade cryptoniscien," Giard and Bonnier) the body is elongated; the antennules are often biramous, with numerous sensory filaments; seven pairs of thoracic legs are present, with coxal plates, and at least the anterior pairs are subchelate; there is no anal tube; the eyes are well developed, sometimes very large. According to Sars, whose views have recently received support from some experiments by Caullery, a third larval stage intervenes, in some if not in all cases, between the two just described. In this stage, formerly described as a distinct genus under the name *Microniscus*, F. Müller, the larva is temporarily parasitic on pelagic Copepoda (Gymnoplea). A certain amount of retrogressive metamorphosis takes place, the appendages are imperfectly segmented, the muscles appear to degenerate, and the pleopods lose their natatory setae. Later, the larva assumes the cryptoniscan form and leaves the Copepod to seek a second host. In those families of the Epicaridea grouped together in the tribe Cryptoniscina, the male becomes sexually mature in the cryptoniscan stage, while the adult female, which, in some if not in all cases, is the same individual in a later stage of development, becomes variously degenerate and may lose all appendages and even all traces of segmentation. In the tribe Bopyrina, where the occurrence of hermaphroditism is doubtful, both sexes pass beyond the crypto-

niscan stage before sexual maturity is reached. The male (Fig. 129, A) develops to the bopyroid stage ("stade bopyrien," Bonnier), characterised by the reduction in size of most of the appendages; antennules and antennae lose their sensory filaments and become almost vestigial, the thoracic legs are shorter and without coxal plates, the pleopods are greatly reduced, without natatory setae, and the eyes are lost or persist only as pigment-spots. The young

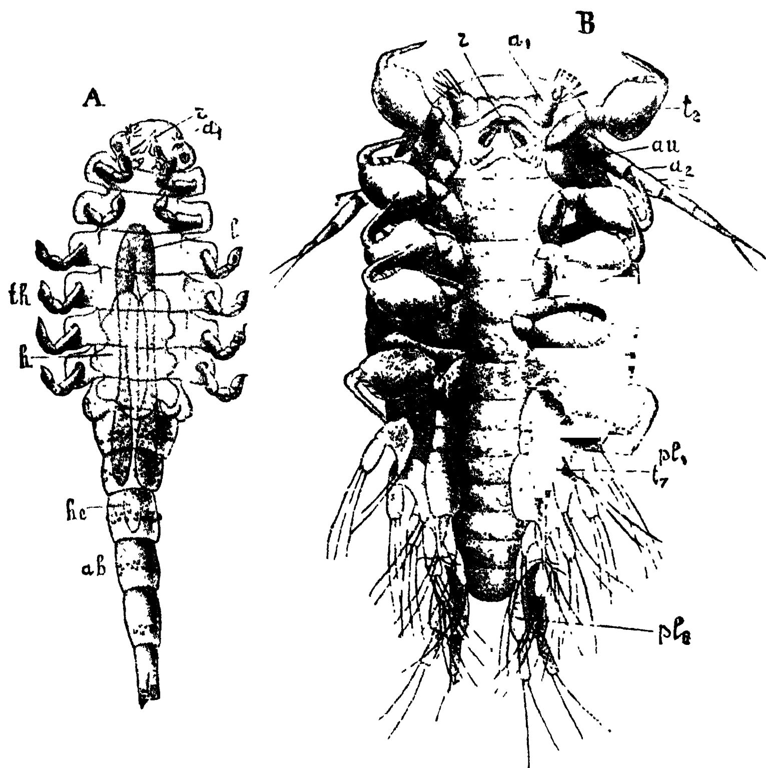


Fig. 129.

A, male of *Cancrion miser* (Entoniscidae). B, larva of *Portunion maenadis* (Entoniscidae) in epicarid stage. a_1, antennule; a_2, antenna; *ab*, abdomen; *au*, eye; *h*, testis; *he*, heart; *l*, hepatic caeca; pl_1-pl_6, the six pairs of abdominal appendages; *r*, oral cone; t_2-t_7, second to seventh pairs of thoracic appendages (the eighth pair are undeveloped at this stage); *th*, thorax. (After Giard and Bonnier, from Korschelt and Heider's *Embryology*.)

post-larval female is generally similar to the male, so that we may speak of a bopyroid stage in both sexes, but the adult female is usually much modified, often asymmetrical and distorted by the great development of ovaries and brood-pouch (Fig. 130). The male is often found attached, like a parasite, to the body of the much larger female (Fig. 124, B).

Remarks on Habits, etc.

The great majority of Isopoda are marine, but the large group of Oniscoidea are terrestrial in their habits, and many of them have developed special organs for aerial respiration, as already described. The Asellidae and Phreatoicidea inhabit fresh water. A very remarkable assemblage of forms have recently been described from subterranean waters in many parts of the world. These include not only freshwater types like Asellidae and

Fig. 130.

Adult female of *Portunion maenadis* (Entoniscidae). A, the brood-chamber partly opened and the oostegites spread out; the abdomen is turned to show the ventral surface. B, the brood-chamber unopened, showing dorsal surface of abdomen. I *r*, the three lobes of the first oostegite on the right side; I *l*, the same on the left side; II *r*, II *l*, second oostegites, right and left; III *r*, III *l*, third oostegites, right and left; IV, fourth oostegite; V *r*, V *l*, fifth oostegites, right and left; *ab*, abdomen; *ae*, vestige of antenna; *ai*, vestige of antennule; ex_2, exopodite of second pleopod; en_3, endopodite of third pleopod; *cg*, head, dilated into a bilobed form by the "cephalogaster"; *h*, cardiac prominence; *mf*, maxilliped; *ov*, ovary; *pl*, pleural lamella of first abdominal somite; *th*, thorax. (After Giard and Bonnier, from Korschelt and Heider's *Embryology*.)

Phreatoicidea, but also members of the Cirolaninae, Anthuridae, and Sphaeromidae, which are otherwise characteristically or exclusively marine in habitat. The number of parasitic forms is very large, including many of the Cymothoidae and the whole of the Epicaridea, the former infesting chiefly fishes and the latter exclusively Crustacea (Ostracodà, Cirripedia, Mysidacea, Isopoda,

including members of the same sub-order, Amphipoda, Euphausiacea, Decapoda). In both groups the parasitic habit is associated with the occurrence of hermaphroditism. The Cymothoidae present a series leading from the predatory, actively swimming Cirolaninae, with mouth-parts adapted for biting, to the sedentary Cymothoinae, with suctorial mouth-parts. Some of the Epicaridea (Entoniscidae) become practically endoparasitic, penetrating into the body of the host, although remaining enveloped by an invagination of the

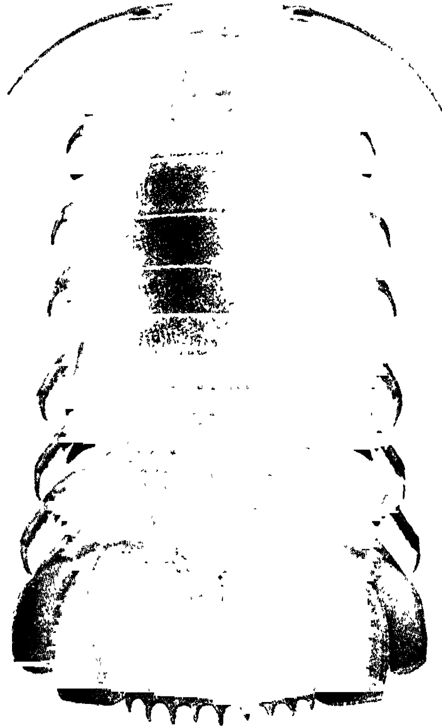


FIG. 131.
Bathynomus giganteus, dorsal view, about three-sevenths of natural size. (After Milne-Edwards and Bouvier.)

integument. The mode of absorbing nutriment by root-like processes penetrating the body of the host, which is found in the Rhizocephala and some Copepoda, appears to be adopted by some of the Liriopsidae.

Some of the smallest Isopoda are found among the Asellota, certain species of which do not exceed 1½ mm. in length when adult. A length of three inches is exceptional in the Order, and *Bathynomus giganteus* (Fig. 131), which reaches nearly eleven inches

in length by five in breadth (270 × 118 mm.), is by far the largest known Isopod.

Palaeontology.

Fossil remains which may be definitely referred to the Isopoda are comparatively rare, and the little that is known of their morphology leaves their systematic position in most cases doubtful and throws no light on the phylogenetic history of the group. No palaeozoic forms can be referred, with any certainty, to this Order,[1] but several genera are known from Secondary rocks. The genus *Urda*, Münster, from the Jurassic of Solenhofen, if it be an Isopod, presents very peculiar characters, having large mandibles projecting in front of the head as in the male *Gnathia*, which it seems to approach also in the number and relative sizes of the body-somites, although differing in the large size of the eyes. *Cyclosphaeroma* (Jurassic) and *Palaega* (Chalk) strongly resemble in general shape the recent Sphaeromidae and Aeginae respectively. Several genera of Sphaeromidae and Oniscoidea are described from Tertiary deposits. A deformation of the carapace of the Brachyuran *Palaeocorystes* from the Greensand has been supposed to indicate the presence of an Epicaridean parasite.

Affinities and Classification.

The close affinity of the Isopoda with the Tanaidacea, and through them with the more primitive members of the Peracaridan division, is clear; they represent the termination of one of the lines of divergence from the caridoid type. The most primitive characters, on the whole, have been retained by the Asellota, which have small and complete coxopodites on the thoracic legs, six distinct segments in the peduncle of the antennule, and sometimes a vestigial exopodite on the same appendage. The Cirolaninae, however, have retained, in *Bathynomus*, a vestige of the inner flagellum on the antennule, and have, in some cases, six segments in the antennal peduncle, while in the more completely segmented abdomen, and probably in the structure of the pleopods, they may claim to be more primitive than the Asellota.

The structure of the Isopoda is so diversified, and the number of forms included in the Order is so large, that their classification is a matter of some difficulty. The system now most generally adopted is that of Prof. G. O. Sars, which is given below with some slight modifications. The tribes (here regarded as sub-orders) into which he divides the Order are for the most part natural groups, but they are of very unequal value. Hansen has pointed out that the

[1] The Devonian *Oxyuropoda*, recently described from Ireland by Carpenter and Swain, is, however, regarded, with considerable probability, as an Isopod.

Asellota stand somewhat apart from the rest, especially as regards the structure of the pleopods. On the other hand, the Epicaridea are closely related to some of the Flabellifera, the systematic value of the modifications due to parasitism having been here as elsewhere somewhat overestimated. The Gnathiidae, again, are an aberrant family whose relation to the more normal Flabellifera is not clear, and the same may perhaps be said of the Anthuridae.

ORDER **Isopoda**, Latreille (1817).

SUB-ORDER 1. **Asellota**, Latreille (1806).

All the abdominal somites coalesced (except in *Stenasellus*); antennal peduncle of six segments; mouth-parts never suctorial; coxopodites of thoracic legs small, the last six pairs freely movable; first pair of pleopods differing in the two sexes, second pair absent in female; uropods sub-terminal, often biramous, styliform.

Family ASELLIDAE. *Asellus*, Geoffroy; *Stenasellus*, Dollfus. Family STENETRIIDAE. *Stenetrium*, Haswell. Family PARASELLIDAE. *Janira*, Leach; *Jaera*, Leach; *Munna*, Boeck; *Desmosoma*, G. O. Sars; *Nannoniscus*, G. O. Sars; *Munnopsis*, M. Sars; *Eurycope*, G. O. Sars; *Acanthocope*, Beddard.

SUB-ORDER 2. **Phreatoicidea**, Stebbing (1893).

Abdominal somites all free; antennal peduncle of five segments; mouth-parts normal; coxopodites of thoracic legs small, the last six pairs movable; first pair of pleopods similar in the two sexes, second pair present in female; uropods sub-terminal, biramous, styliform; body more or less laterally compressed, amphipod-like.

Family PHREATOICIDAE. *Phreatoicus*, Chilton (Fig. 119); *Phreatoicopsis*, Spencer and Hall; *Phreatoicoides*, Sayce.

SUB-ORDER 3. **Flabellifera**, G. O. Sars (1882).

Abdominal somites free or more or less coalesced; antennal peduncle rarely with six segments; mouth-parts often suctorial; coxopodites of thoracic legs more or less expanded into coxal plates, partially or completely fused with body; first pair of pleopods similar in the two sexes, second pair present in female; uropods lateral, generally biramous, lamellar, forming a caudal fan.

Family GNATHIIDAE. *Gnathia*, Leach (Fig. 121) (=*Anceus*, Risso) (♂), and *Praniza*, Latreille (♀ and yg.) Family ANTHURIDAE. *Anthura*, Leach; *Cyathura*, Norman and Stebbing; *Paranthura*, Bate and Westwood; *Cruregens*, Chilton. Family CYMOTHOIDAE. (The following sub-families are often ranked as families.) Sub-Family CIROLANINAE (EURYDICINAE). *Cirolana*, Leach; *Eurydice*, Leach; *Conilera*, Leach; *Bathynomus*, A. Milne-Edwards (Fig. 131). Sub-Family ANUROPODINAE. *Anuropus*, Beddard; *Branchuropus*, Moore. Sub-Family EXCORALLANINAE. *Excorallana*, Stebbing. Sub-Family CORALLANINAE. *Corallana*, Dana;

Alcirona, Hansen; *Tachaea*, Schiodte and Meinert. Sub-Family ARGATHONINAE. *Argathona*, Stebbing. Sub-Family BARYBROTINAE. *Barybrotes*, Schiodte and Meinert. Sub-Family AEGINAE. *Aega*, Leach; *Rocinela*, Leach. Sub-Family CYMOTHOINAE. *Cymothoa*, Fabricius; *Ceratothoa*, Dana; *Meinertia*, Stebbing; *Nerocila*, Leach. Family SEROLIDAE. *Serolis*, Leach. Family SPHAEROMIDAE. Sub-Family LIMNORIINAE. *Limnoria*, Leach. Sub-Family SPHAEROMINAE. *Sphaeroma*, Latreille; *Cymodoce*, Leach; *Dynamene*, Leach; *Campecopea*, Leach; *Monolistra*, Gerstaecker; *Vireia*, Dollfus; *Cassidina*, H. Milne-Edwards; *Ancinus*, H. Milne-Edwards. Sub-Family PLAKARTHRIINAE. *Plakarthrium*, Chilton.

SUB-ORDER 4. **Valvifera,** G. O. Sars (1882).

Abdominal somites more or less coalesced; antennal peduncle of five segments; mouth-parts normal; coxopodites of thoracic legs expanded into coxal plates, rarely quite concealed beneath pleural plates; first pair of pleopods similar in the two sexes (except in *Pseudidothea*), second pair present in female; uropods lateral, opercular, folded inwards over pleopods, exopodite vestigial or absent.

Family IDOTEIDAE. *Idotea*, Fabricius; *Chiridotea*, Harger; *Glyptonotus*, Eights. Family CHAETILIIDAE. *Chaetilia*, Dana. Family PSEUDIDOTHEIDAE. *Pseudidothea*, Ohlin. Family HOLOGNATHIDAE. *Holognathus*, G. M. Thomson. Family AMESOPODIDAE. *Amesopous*, Stebbing. Family ARCTURIDAE (ASTACILLIDAE). *Arcturus*, Latreille; *Astacilla*, Cordiner; *Anarcturus*, zur Strassen.

SUB-ORDER 5. **Oniscoidea,** G. O. Sars (1882).

Abdominal somites rarely coalesced; antennules minute; antennal peduncle of five segments; mouth-parts not suctorial, mandibles without palp, maxillae reduced; coxopodites of thoracic legs expanded into coxal plates, usually completely coalesced with body, rarely defined by sutures; first pair of pleopods usually differing in the two sexes, sometimes absent, second pair present in female; uropods sub-terminal, generally biramous and styliform; terrestrial in habits, often with pseudo-tracheae in pleopods.

Family LIGIIDAE. *Ligia*, Fabricius; *Ligidium*, Brandt. Family TRICHONISCIDAE. *Trichoniscus*, Brandt; *Haplophthalmus*, Schiodte. Family TYLIDAE. *Tylos*, Audouin; *Helleria*, von Ebner. Family ONISCIDAE. Sub-Family SCYPHACINAE. *Scyphax*, Dana. Sub-Family ONISCINAE. *Oniscus*, Linnaeus; *Porcellio*, Latreille (Fig. 118). Sub-Family ARMADILLIDINAE. *Armadillidium*, Brandt; *Cubaris*, Brandt (= *Armadillo*, Latreille).

SUB-ORDER 6. **Epicaridea,** Latreille (1831).

Parasitic forms in which the adult females are greatly modified, often asymmetrical, sometimes without appendages and without segmentation of the body; mouth-parts suctorial, with simple piercing mandibles, maxillulae and maxillae vestigial or absent; pleopods, when present, without sexual modification; uropods uniramous, very small, often absent; late

larval (cryptoniscan) stage with abdominal somites distinct, with coxal plates on thoracic somites, with uni- or biramous pleopods, and with terminal, biramous, styliform uropods; parasitic on Crustacea.

TRIBE 1. CRYPTONISCINA.

Male becomes mature in cryptoniscan stage; protandrous hermaphroditism probably universal; brood-pouch not formed by oostegites; first larval stage with biramous pleopods.

Family HEMIONISCIDAE. *Hemioniscus*, Buchholz (on Cirripedia). Family CYPRONISCIDAE. *Cyproniscus*, Kossmann (on Ostracoda). Family LIRIOPSIDAE. *Liriopsis*, Schultze; *Danalia*, Giard (on Rhizocephala). Family ASCONISCIDAE. *Asconiscus*, G. O. Sars (on Mysidacea). Family CRINONISCIDAE. *Crinoniscus*, Pérez (on Cirripedia). Family PODASCONIDAE. *Podascon*, Giard and Bonnier (on Amphipoda). Family CABIROPSIDAE. *Cabirops*, Kossmann; *Clypeoniscus*, Giard and Bonnier (on Isopoda).

TRIBE 2. BOPYRINA.

Male becomes mature in bopyroid stage; sexes probably always distinct; brood-pouch formed by oostegites; first larval stage with uniramous pleopods.

Family DAJIDAE. *Dajus*, Kroyer; *Notophryxus*, G. O. Sars (on Mysidacea and Euphausiacea). Family BOPYRIDAE (including PHRYXIDAE of Bonnier). *Bopyrus*, Latreille; *Gyge*, Cornalia and Panceri (Fig. 124); *Phryxus*, Rathke (on Decapoda). Family ENTONISCIDAE. *Entoniscus*, F. Muller; *Portunion*, Giard and Bonnier (Fig. 130); *Priapion*, Giard and Bonnier; *Cancrion*, Giard and Bonnier (on Brachyura).

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CHAPTER XIII

THE AMPHIPODA

Order **Amphipoda**, Latreille (1816).
Sub-Order 1. **Gammaridea.**
,, 2. **Hyperiidea.**
,, 3. **Caprellidea.**
,, 4. **Ingolfiellidea.**

Definition.—Peracarida in which there is no distinct carapace, but the first thoracic somite (more rarely also the second) is coalesced with the head; the telson is usually distinct from the last somite; eyes sessile; antennules often biramous; antennae without exopodite, the peduncle typically of five segments; thoracic limbs without exopodites; first pair modified as maxillipeds, coalesced at the base, without epipodite; remaining pairs variously modified, the second and third commonly prehensile, coxopodites always short, usually expanded as coxal plates, movably connected with the body; branchial appendages on inner side of coxopodites of some of the thoracic limbs; pleopods, when fully developed, divided into two sets, the first three pairs with multiarticulate rami, the last two pairs generally similar to the uropods, with unsegmented rami; no sexual modification of pleopods; the young leave the brood-pouch provided with all the appendages of the adult.

Historical.—In establishing the order Amphipoda (1816) Latreille excluded from it the genus *Cyamus*, which he referred to the Isopoda. Later, he established a separate order, Laemodipoda, for *Caprella* and *Cyamus*, placing it between the Amphipoda and Isopoda. This arrangement was adopted by H. Milne-Edwards, who further divided the Amphipoda into two families, Gammarina and Hyperina. Kröyer, in 1843, showed very clearly that the Laemodipoda present only an extreme modification of the Amphipod type. Dana, in 1852, subdivided the Order into three groups —Caprellidea, Gammaridea, and Hyperiidea, a classification which has held its own to the present time. There appear to be no sufficient grounds for establishing the additional divisions of

Synopidea, Bovallius, and Subhyperini, Della Valle, and still less reason for the inclusion of the Tanaidacea, advocated by Gerstaecker. On the other hand, the very remarkable genus *Ingolfiella*, Hansen, may conveniently, for the present, be kept apart in the sub-order Ingolfiellina which Hansen has established for it. Among the more important contributions to our knowledge of the group mentioned in the list of literature at the end of this chapter, attention may be called to Spence Bate's British Museum Catalogue, Spence Bate and Westwood's Monograph of the British species, and to the works of Boeck, Bovallius, Claus, and Delage. As with so many other groups of Crustacea, the memoirs by G. O. Sars are numerous and

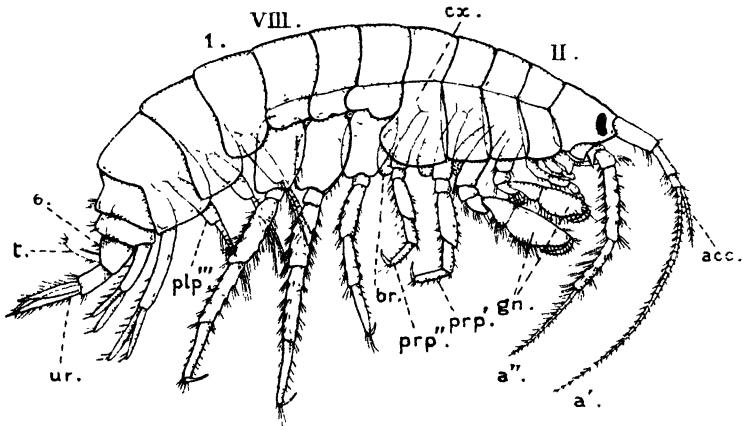


Fig. 132

Gammarus locusta, ♂, from the side. × 4. *a'*, antennule; *a''*, antenna; *acc*, accessory (inner) flagellum of antennule; *br*, branchia; *cx*, coxal plate; *gn*, gnathopods; *plp'''*, pleopod of third pair; *prp'*, *prp''*, first and second peraeopods (fourth and fifth thoracic appendages); *t*, telson; *ur*, uropod (sixth abdominal appendage); II, VIII, second and eighth thoracic somites; 1, 6, first and sixth abdominal somites. (After G. O. Sars.)

of the first importance. Della Valle's Monograph is valuable for anatomical and biological details, but the systematic part of the work is to be used with caution. The bibliographical history of the Order has been given at length in the admirable Introduction to Stebbing's Report on the "Challenger" collection, and the same author has recently completed a masterly revision of the Gammaridea for the *Tierreich*. P. Mayer's Monograph and his later memoirs on the Caprellidea will not soon be superseded as the chief sources of information on that sub-order.

Morphology.

The body of a typical Amphipod, such as *Gammarus* (Fig. 132), is laterally compressed, with the abdomen of considerable size and

flexed ventrally between the third and fourth somites. The large coxal plates (*cx*) on the thoracic somites projecting downwards increase the depth of the body and add to the appearance of lateral compression. Even within the sub-order Gammaridea, however, this typical form is sometimes departed from by attenuation of the body or by its dorso-ventral flattening, which, in *Pereionotus* and some other genera, is carried so far as to give the general appearance of an Isopod. In the sub-orders Hyperiidea and Caprellidea the range of modification is much greater. The Hyperiidea, while departing the less widely, on the whole, from the typical form, include such extreme types as the balloon-like *Mimonectes* and the almost linear *Rhabdosoma* (Fig. 133). The Caprellidea differ from both the other sub-orders in the vestigial condition of the abdomen

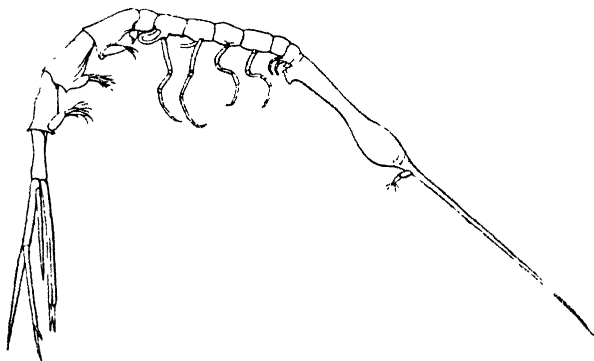


Fig. 133.
Rhabdosoma piratum (Hyperiidea). (After Stebbing, from [illegible] *Brit.*)

and the coalescence of the second thoracic somite with the head; they comprise two families of widely different facies, the filiform Caprellidae (Fig. 134) and the flattened, Isopod like whale-lice, Cyamidae (Fig. 135).

The eyes, when present, are sessile on the sides of the head. Sometimes they coalesce in the median line, and in some Oedicerotidae the fused eyes are borne on a projecting frontal lobe. In *Ingolfiella*, distinct eye-lobes are present (although the eyes are apparently deficient), defined by suture-lines from the antero-lateral margins of the head-region. It is possible that these lobes may represent the eye-lobes of Tanaidacea and the ocular peduncles of more primitive Malacostraca, though the great specialisation of *Ingolfiella* in other respects is rather against this view.

Appendages.—The *antennules* (Fig. 132, *a'*) consist typically of a peduncle of three segments carrying two flagella. The outer flagellum is usually long and multiarticulate, while the inner (*acc*)

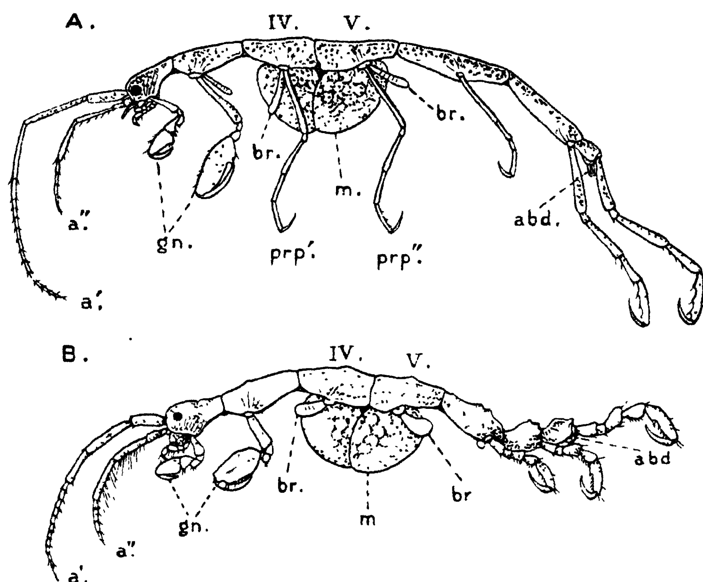


Fig. 134.

A. *Phtisica marina*, ♀, × 5. B. *Caprella linearis*, ♀, × 7 (Caprellidea). *a'*, antennule; *a''* antenna; *abd*, vestigial abdomen, with small appendages in A; *br*, branchiae; *gn*, gnathopods (second and third thoracic appendages); *m*, brood-pouch; *prp'*, *prp''*, first and second peraeopods (fourth and fifth thoracic appendages), wanting in B; IV, V, fourth and fifth thoracic somites. (After G. O. Sars.)

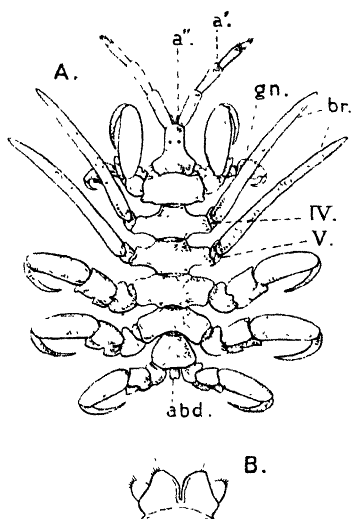


Fig. 135.

Paraegamus boopis. A, male, dorsal view, × 4. B, maxillipeds. *a'*, antennule; *a''*, antenna; *abd*, vestigial abdomen; *br*, branchiae; *gn*, gnathopods (second and third thoracic appendages); IV, V, fourth and fifth thoracic somites. (After G. O. Sars.)

is frequently absent, and, when present, is generally inconspicuous and composed of few segments.

The *antennae* (Fig. 132, *a*″) when fully developed have a peduncle of five segments and a more or less elongated flagellum. A scale or exopodite is never developed. A conspicuous conical or spiniform tubercle on the *second* joint of the peduncle bears the aperture of the antennal gland, indicating that the five segments of

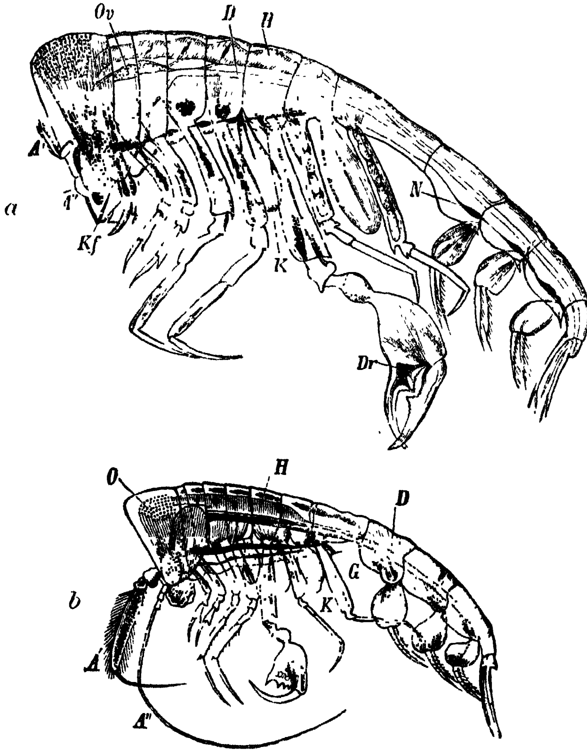


Fig. 136.

Phronima sedentaria. *a*, female; *b*, male. *A*′, antennule; *A*″, antenna; *D*, intestine; *I r*, gland in chela of sixth thoracic appendage; *G*, genital aperture of male; *H*, heart; *K*, branchia; *Kf*, mandible; *N*, ventral nerve-chain; *O*, eye; *Ov*, ovary. (From Claus's *Textbook*.)

the peduncle must be derived from the six-segmented condition by a coalescence of two segments distal to the gland-opening, probably the third and fourth. In many cases the antennules and antennae are more strongly-developed in the male than in the female sex, and bear more numerous sensory setae. In some Hyperiidea (Fig. 136) the antenna, though well developed in the male, is represented in the female only by a rounded tubercle containing the antennal gland on the front of the head. In some cases the

antennae have almost a pediform character, the segments of the peduncle being long and stout and the flagellum reduced, as in the Amphithoidae and allied families and conspicuously in the Corophiidae.

The *mandibles* have usually the typical Peracaridan structure with molar process, serrated incisor process, lacinia mobilis on the left mandible or on both, a row of spines, and a palp of three segments, but any of these parts may be modified or absent. The palp, in particular, may be present or absent in genera otherwise very closely related.

The *maxillulae* (Fig. 137, A) are remarkable in that they commonly exceed the maxillae in size and complexity of structure. Two endites are present, springing, according to Hansen's interpretation, from the first and third segments, and the fourth and

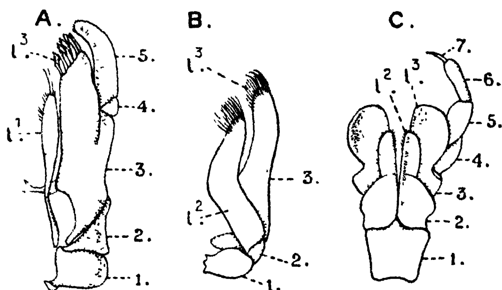


FIG. 137.

A, maxillula, B, maxilla, C, maxillipeds, of *Socarnes bidenticulatus* (Gammaridea). The distal segments of the left maxilliped are omitted. 1-7, segments of the appendages; l^1-l^3, endites of the respective segments. (After Hansen.)

fifth segments form a "palp" which is turned forwards and inwards, resembling in appearance, and no doubt also in function, a third endite. The *maxillae* (Fig. 137, B) are small in size and simple in form, consisting mainly of two plates which, according to Hansen, are the endites of the second and third segments. The *lower lip* may attain to greater complexity than in most other divisions of the Malacostraca and its modifications are of some systematic importance. The two main lobes (paragnatha) of which it elsewhere consists are in many cases supplemented by a pair of accessory lobes lying between them, while the main lobes themselves may be produced at the outer corners or each divided by incision into two as in the Amphithoidae.

The first thoracic appendages or *maxillipeds* (Fig. 137, C) are always coalesced at the base, the coxopodites fusing to form an unpaired plate. The basipodite is produced into an endite, usually referred to as the "inner plate" (l^2), which may be armed with teeth, spines, or setae, but does not carry coupling-hooks. The

ischiopodite also bears an endite (the "outer plate," l^3), and the remaining four segments form the "palp." The palp is not unfrequently abbreviated by the suppression of one or two of its segments, and the coalescence of the proximal region may involve the basipodites partially or completely. Both these modifications are carried to an extreme in the Hyperiidea (Fig. 138), where the maxillipeds are represented by an unpaired plate carrying a pair of movable, unjointed appendages, representing in all probability the ischiopodites with their endites, and a median process corresponding to the coalesced inner plates. In the Cyamidae the maxillipeds are sometimes of normal structure, but they may be greatly reduced (Fig. 135, B), and in *Platycyamus* they are represented only by an unpaired plate without any trace of articulations. In *Cyamus nodosus* the interesting observation has been made that the young animals taken from the brood-pouch have well-developed maxillipeds with the full number of segments, although in the adults of this species they are reduced to a pair of unjointed appendages attached to the common basal plate.



FIG. 138. Reduced maxillipeds of *Hyperia galba*. (After G. O. Sars.)

Of the remaining seven pairs of thoracic appendages, the first two are commonly, though not invariably, modified for prehension, and are distinguished as *gnathopods* (Figs. 132, 134, 135, *gn*) from the remaining five pairs, the *peraeopods*, which are generally organs of locomotion. Each limb consists of the usual seven segments. The coxopodite is always short, but is usually expanded externally to form a *coxal plate* (Fig. 132, *cx*), sometimes of great size; internally it bears the branchial plate (*br*) and oostegite when these are present. In the Caprellidea and Ingolfiellidea the coxopodite remains small. In some Hyperiidea it is entirely coalesced with the somite. The basipodite is usually more or less elongated; the ischiopodite, on the other hand, generally short, contrary to the rule among the Isopoda. The terminal claw is usually coalesced with the dactylopodite.

The lateral compression of the body in most Amphipoda has lead to a separation of the thoracic legs into an anterior group of four (the two gnathopods and the first two paraeopods) and a posterior of three, which are opposed to each other in the direction of the principal articulations. In the case of the anterior group the limb is bent forwards at the articulation between the ischiopodite and meropodite, and backwards at that between meropodite and carpopodite, and the dactylopodite points backwards; in the posterior group these directions are reversed and the dactylopodite points forwards except in the case of certain Gammaridea, where the direction of the dactylopodite (but not of the other segments)

is reversed.[1] The distinctness of these two groups is further expressed by the relations of the coxal plates. Where these are small or of moderate size they are of similar form throughout the series, but when, as in many Gammaridea (Fig. 132), enlargement takes place, it is mainly the first four that become expanded so as to cover from the outside the basipodites, or even the whole limb; the last three coxal plates in this case generally remain small and their place in protecting the gills within is taken by the expanded basipodites. The two pairs of legs following the gnathopods (the fourth and fifth of the thoracic series) are, among the Gammaridea (Fig. 132, *prp′*, *prp″*), not unfrequently more or less different from the succeeding pairs. In the Caprellidea, these two pairs are vestigial or absent except in the genus *Phtisica* (*Proto*) (Fig. 134, A) and its immediate allies.

In the gnathopods of the Gammaridea every gradation may be traced from the simple, non-prehensile leg to the well-formed, sub-chelate, or perfectly chelate type, and even to more complex forms, as in *Leucothoe* and *Aora*. The gnathopods of *Ingolfiella* have a very unusual structure, the propodite and dactylopodite together forming the movable finger which is opposed to the expanded carpopodite. Some of the peraeopods may show modification for prehensile purposes in Gammaridea, and in *Polycheria* all of them are sub-chelate. In the Hyperiidea much greater variety occurs, and any of the peraeopods except the last pair may be transformed into a chela, sometimes of large size (Fig. 136). The gnathopods, in this group, are always small. In the Caprellidae (Fig. 134) the gnathopods are sub-chelate and the last three pairs of peraeopods are also fitted for grasping. A point of interest with regard to these peraeopods is the existence in the basipodite of a definite "fracture-plane" at which the limb breaks off in autotomy. A similar fracture-plane is found in the legs of many Decapoda, where the habit of autotomy is highly developed.

The *branchiae* (Figs. 132, 134, 135, *br*; Fig. 136, *K*) are attached to the inner surfaces of the coxopodites, near the posterior border. They are generally vesicular or lamellar in form, and in some Gammaridea the respiratory surface is increased by numerous transverse ridges or folds. In some species of Cyamidae (*Cyamus physeteris*) the branchiae are ramified. Accessory branchiae occur in certain Gammaridae and Talitridae on some of the thoracic limbs and also on the first abdominal somite. The greatest number of branchiae is six pairs, occurring on the last six thoracic limbs in many Gammaridea. The number

[1] The correlation between the lateral compression of the body and this grouping of the legs is well illustrated by comparison with *Phreatoicus*, the only Isopod where the body is laterally compressed and where the legs are divided into two groups exactly as in Amphipods.

in this sub-order, however, is not unfrequently reduced to five, four, or even three pairs. In Hyperiidea the last pair of thoracic legs never carry branchiae and the number may vary from five to two pairs. In Caprellidea as a rule only two pairs of branchiae are present, on the fourth and fifth thoracic somites, but in some genera of Caprellidae there is an additional pair on the third somite (that of the second gnathopods).

The *oostegites* spring from the inner surface of the coxopodites on the proximal side of the branchial plates. Four pairs are commonly present, on the third to the sixth thoracic somites, but the number may be reduced. In the Caprellidea (Fig. 134, *m*) two pairs only exist, on the fourth and fifth somites, but in addition a pair of small valvular appendages covering the external apertures of the oviducts on the sixth somite are probably to be regarded as vestiges of a third pair. Vestigial oostegites are stated to occur normally in the male sex in a few cases (*e.g.* *Cyamus globicipitis* and *Synurella polonica*).

It is very characteristic of the Amphipoda that the abdominal appendages are sharply divided into two groups differing in structure. In the majority of Gammaridea (Fig. 132) and Hyperiidea (Fig. 136) all the six pairs are present, the first three pairs are turned forwards and consist of a peduncle carrying two subequal rami, each of which is multiarticulate and fringed with long setae; the inner side of the peduncle bears distally a number of retinacula, and the first joint of the endopodite has internally one or two peculiar "cleft spines" which no doubt serve the same purpose of coupling together the pair of appendages. These limbs are the chief natatory organs among Amphipoda, and they also serve when the animal is at rest to maintain a current of water over the gills. The last three pairs of abdominal appendages are directed backwards and are generally similar to each other, so that the name *uropods* is commonly used to include them all, though in not a few cases the last pair retain, in details of form and size, some mark of that differentiation from the preceding appendages which they show in other orders of the Malacostraca. As a rule, the three pairs are biramous; not unfrequently the exopodite of the last pair consists of two segments, but except for this the rami of all are unjointed. Sexual differences not unfrequently occur in the size and structure of the last pair, but in no Amphipoda are any of the pleopods modified as copulatory organs. The abdomen of most Caprellidea is unsegmented and may bear vestigial appendages to the number of three pairs (Fig. 134, *abd*). An interesting link with the normal Amphipoda is constituted by the genus *Cercops*, where five distinct somites and a terminal piece (perhaps the telson) are present. The first and second somites bear, in the male sex only, minute filiform appendages of two

segments which appear to correspond to the first and second pleopods of the normal type, while the fourth and fifth somites carry in both sexes stout two-segmented limbs answering to the first and second uropods. In most other Caprellidae the rudimentary appendages are more fully developed in the male than in the female sex, but in a few the abdomen is quite without appendages. In the male Cyamidae a median appendage is present which seems to result from the fusion of a pair of uropods. In *Ingolfiella* the first three pairs of abdominal limbs are represented by small triangular plates, sometimes with a minute basal segment, without any trace of rami. The last pair is vestigial.

Alimentary System.—The alimentary canal of the Amphipoda appears to differ from that of most Isopoda in the much greater development of the mid-gut region, which forms the greater part of its length. The stomodaeum forms a masticatory or triturating stomach, the structure of which appears to be fairly uniform throughout the Gammaridea and Caprellidea, and to be more or less simplified in the Hyperiidea. When fully developed it presents anteriorly two lateral ridges projecting into the cavity, armed with spines and stiff setae. These ridges are moved by powerful muscles passing outwards to the body-wall on either side, and appear to be the most important instruments of trituration. Posterior to these are two pairs of setose ridges running more or less transversely, while in the floor of the cavity is a strong ridge ending behind in a free tongue-like process and carrying anteriorly four comb-like rows of iridescent setae. The chitinous lining of the stomodaeum projects backwards into the beginning of the mid-gut as a cuticular funnel. In *Phronima*, where the apparatus appears to be adapted for straining rather than for masticating the food, the whole stomach is telescoped for a little way into the capacious mid-gut. The hepatic caeca are generally four in number and of considerable length, but in a few genera of Gammaridea and in most Hyperiidea only one pair is present, while in the Caprellidea the ventral pair and in *Phronima* both pairs remain rudimentary. Just above the point where the hepatic caeca communicate with the gut by a common aperture on each side, a short dorsal, forwardly directed caecum, unpaired in Gammaridea, paired in Hyperiidea and Caprellidea, arises from the anterior end of the mid-gut. At the posterior end of the mid-gut, at its junction with the proctodaeum, a second pair of caeca of very varying size is commonly present in the Gammaridea. In a few cases only a single unpaired caecum is present (*Melita*), and in *Synurella*, though two tubes are present in the young, that on the right side atrophies and only that on the left persists. Similar paired caeca are only exceptionally present in Hyperiidea (*Vibilia*) and Caprellidea (*Caprella*). To these posterior caeca of the mid-gut an excretory function has been

attributed, mainly on the ground that they sometimes contain calcareous concretions; as they are outgrowths of the mesenteron, it is impossible to regard them as homologous with the Malpighian vessels of insects. In the Hyperiidea the anterior part of the mid-gut may be dilated while the posterior part remains narrow. It is stated to be lined by a very delicate cuticle of non-chitinous nature. The proctodaeum is short, rarely reaching forward to the posterior limit of the thorax, or, in the Caprellidea, into the penultimate thoracic somite. An "anal gland" in the form of a small diverticulum is described in *Synurella*.

Circulatory System.—The circulatory system of Amphipoda is remarkable for the imperfect development of the arterial vessels and the consequent lacunar character of the greater part of the circulation; as compared with that of the Isopoda it differs also in the position of the tubular heart, which extends through the greater part of the thoracic somites but does not reach the abdomen. It lies in a spacious pericardium which may extend backwards into the abdomen. Three pairs of ostia are present in most Gammaridea, but *Corophium* has only one pair; the Caprellidea have three pairs; in the Hyperiidea only two pairs are present as a rule, but in *Phronima*, although the male has only two, the female has three pairs. The heart is continued at either end into the anterior and posterior aortae, which are defined by valves. In addition, a pair of arteries supplying the eyes and adjacent parts may arise from its anterior end, but only in the Hyperiidea are there two or three pairs of lateral arteries arising from the heart in the thorax and comparable to the thoracic arteries of the Isopoda. The anterior aorta is stated to divide in the median plane to encircle the brain. in a "pericerebral vascular ring" very characteristic of the order, with which is connected (except in Caprellidae) an oesophageal ring similar to that of the Isopoda. It seems probable, however, that these rings are rather lacunar spaces than well-defined vessels. There is no trace of the subneural artery commonly developed in Isopods, the oesophageal ring opening posteriorly into the great ventral sinus which extends through the whole length of the body, and into which the posterior aorta also empties its contents at or near the end of the abdomen. Except perhaps in those forms (Hyperiidea) which possess lateral thoracic arteries, the appendages of the thorax and abdomen receive their blood-supply from this ventral sinus. Within the appendages the afferent blood-streams are contained in well-marked vessels which send branches to the gills. The efferent vessels of the appendages unite to form in each somite (except sometimes in the abdomen) a pair of pericardial vessels by which the blood is returned to the heart.

In comparing the circulatory system with that of the Isopods, it is clear that the course followed by the blood in the abdominal

region is similar in both cases, the ventral sinus sending blood into the appendages, from which it is returned to the pericardium by the centripetal sinuses; the ventral sinus in Amphipoda receiving, however, arterial blood directly from the posterior aorta. In the thorax the course of the circulation is very different.

In the Isopoda the appendages receive blood directly from the heart by means of the lateral thoracic arteries and return it to the ventral or lateral thoracic sinuses; in the Amphipoda, on the other hand, the limbs with their branchial plates receive blood from the ventral sinus and return it directly to the pericardium by the pericardial vessels. The ventral sinus of the Amphipoda, however, does not wholly correspond to the ventral or lateral sinuses of the Isopoda, but, since it receives arterial blood both anteriorly and posteriorly from the aorta, represents in part also the sternal system of arteries in the last-named group, while the homologues of the thoracic afferent pericardial vessels of the Amphipoda are to be found in the blood-stream which enters the pericardium of the Isopoda through the minute apertures at its anterior end.

Excretory System.—No trace of a maxillary gland has been recognised in any Amphipod. The antennal gland, on the other hand, is rarely, if ever, wanting. It has been most fully studied in certain freshwater Gammaridae, where it presents the usual divisions of end-sac, convoluted tube, and duct, the latter being sometimes dilated into a vesicle. The gland is usually contained within the first segment of the antenna, and its external aperture is at the tip of a conical or spiniform process of the second segment. "Coxal glands" are described as present in all the thoracic and the first three abdominal appendages of *Gammarus*. They consist of small groups of cells, without duct or opening to the exterior, rendered visible in the living animal by feeding with carmine.

Dermal Glands.—In many Amphipoda there are found groups of unicellular glands lying in the thoracic appendages and opening by fine ducts at or near the extremity of the limb. Among the Gammaridea such glands are well developed in the Photidae, Aoridae, Amphithoidae, Jassidae, Corophiidae, and some of the allied families, where they are confined to the fourth and fifth thoracic appendages, lying mainly in the basipodite and connected with a duct which opens on the tip of the claw. In the Ampeliscidae similar glands occur but are more widely distributed on the other appendages of the body. In all the families named the glands secrete a cementing material which is used in building up with particles of mud or sand or fragments of weed the cases or tubes in which the animals live. In the Talitridae, which burrow in sand, glands of similar structure are scattered over the surface of the body and appear to secrete a mucinous substance which lines the burrows. Glands of very similar structure to those just

described, but apparently with different functions, occur in many Hyperiidea. In the Phronimidae, where they have been most carefully studied, they occur in all the thoracic legs, and the ducts open at the end of the limb or, in the case of the antepenultimate pair, on teeth of the palmar edge of the chela. It is supposed that in this case they act as poison-glands. In many Caprellidae groups of gland-cells also supposed to secrete a poison are present in the hand of the second gnathopods, their ducts opening on a prominent tooth of the palmar edge. Finally, glands of similar structure may be found, as in many other Crustacea, in the oral appendages and on the oesophageal walls, and are supposed to be salivary in function.

Nervous System.—The ventral nerve-chain presents, in the majority of the Gammaridea, twelve pairs of ganglia connected by double longitudinal commissures, the sub-oesophageal supplying the mouth-parts, followed by seven corresponding to the free thoracic somites and four abdominal ganglia; but the number may be reduced, especially among the Hyperiidea, by the coalescence of one or two of the anterior thoracic with the sub-oesophageal ganglia, the fusion of the last two thoracic, and the restriction of the abdominal ganglia to three pairs. In the Caprellidea, though four pairs of abdominal ganglia may be distinct in the young, they become in the adult fused into a single mass approximated to the last thoracic ganglion and lying in the penultimate thoracic somite. In *Phronima* the nerves to the mouth-parts arise from the oesophageal commissures close to the under-side of the brain. A post-oral antennal commissure such as exists in the Isopoda is perhaps indicated by the presence (in Gammaridea and Caprellidae) of a median foramen piercing the sub-oesophageal ganglionic complex near its anterior margin and giving passage to an unpaired strand of muscle running between the lower surface of the stomach and the lower lip.

Sense-Organs.—The paired *eyes* of the Gammaridea show great diversity of size and disposition. They are rarely so large as to occupy the greater part of the surface of the head (*Trischizostoma*), while on the other hand they are in not a few cases quite vestigial or apparently absent. In the Oedicerotidae, as already mentioned, they are coalesced to form a single organ which is advanced to the front of the rostral process, and in a few cases (*Tiron*, *Synopia*) a pair of small accessory eyes are placed below the main eyes. This leads to the very remarkable condition found in the Ampeliscidae, which possess two pairs of eyes, each of which is made up of numerous ommatidia differing only in details from those forming the eyes of other Amphipoda, underlying a single lenticular thickening of the cuticle.

In the Caprellidea the eyes are always small, but in the

majority of the Hyperiidea (Fig. 136, *O*) they are enormously enlarged, occupying nearly the whole surface of the head. In this case each eye is commonly divided into two parts, the dorsal differing in the great elongation of the crystalline cones and in other details from the lateral division. Apart from the Ampeliscidae, the eyes of the Amphipoda are characterised by the fact that the corneal covering is not facceted, or, in other words, that corneal lenses are not formed.

In addition to "sensory filaments" of the usual type borne by the main flagellum of the antennule, and sometimes particularly numerous on the enlarged proximal segment of the flagellum (Lysianassidae, Hyperiidea), many Gammaridea have on the antennae, and sometimes on the antennules, peculiar organs known as *calceoli*. These are, in the simplest cases, little flattened vesicles attached by a narrow stalk, but in some the structure is more complex. They are often, but not always, confined to the male sex, and have been variously interpreted as olfactory or auditory organs, as adhesive suckers, and even as sexual ornaments.

A pair of statocysts have been described in connection with the anterior part of the brain in Oxycephalidae.

Reproductive System.—The paired ovaries and testes are of simple tubular form and lie in the thoracic region. The testes are continued posteriorly into short vasa deferentia which may be slightly dilated into seminal vesicles and open on short papillae on the sternum of the last thoracic somite. The oviduct leaves the ovary at about the middle of its length and opens on the inner surface of the fifth coxal plate (sixth thoracic somite). It is stated that an actual opening does not exist until the moment when the eggs are extruded. The spermatozoa consist of a slender rod-like head, to which a filiform tail, stated to exhibit vermiform movements in some cases, is attached at an acute angle. Definite spermatophores are not formed, at least in the majority of Amphipoda. The spermatozoa are deposited on the ventral surface of the body of the female immediately before the eggs are extruded, and fertilisation is external. The occurrence of ova within the testis has been observed in species of *Orchestia*, where it is perhaps universal in young individuals.

Development.

Segmentation is at first total, later becoming superficial, with early differentiation of the blastoderm on the ventral side. The teloblastic mode of growth in the post-naupliar region of the embryo which occurs in many Isopoda and Mysidacea does not present itself.

A "dorsal organ" is early developed as a median thickening

of the ectoderm, the cells of which become pyriform, projecting inwards and connected with the exterior by a narrow neck. The larval cuticle, which is formed soon after the differentiation of appendages has begun, remains adherent to the dorsal organ after separating from the rest of the ectoderm. Later, the cells lose their apparently glandular character and become invaginated as a thin-walled vesicle, which persists after the embryo is freed from the egg-membrane.

The dorsal curvature of the blastoderm as it lies upon the spherical surface of the yolk is early exchanged for a ventral curvature as the abdominal region of the developing embryo becomes folded downwards and forwards. The embryo is not liberated from the egg-membrane until the body and appendages have assumed more or less their final form. The young, however, remain within the marsupium for some time longer, leaving it finally only at the ecdysis which precedes the next act of oviposition. The accounts of some older writers, according to which the young after leaving the marsupium of the parent returned to it for shelter when alarmed, have not been confirmed by any modern observer.

The post-embryonic development in most Amphipoda consists mainly in the gradual assumption of secondary sexual characters and other features of subordinate importance. Only in the Hyperiidea, and notably in the Platyscelidae, do the changes of form occurring after the young leave the brood-pouch deserve the name of metamorphosis.

REMARKS ON HABITS, ETC.

The Hyperiidea and Caprellidea are exclusively marine (the reported occurrence of a Caprellid in the Lake of Geneva rests on insufficient evidence), as are also the great majority of the Gammaridea. The Hyperiidea are pelagic in habitat, sometimes ranging from the surface to great depths, and having often an exceedingly wide horizontal distribution. The Caprellidea, though for the most part inhabiting shallow water and almost or quite without the power of swimming, include some species of almost cosmopolitan range. The Ingolfiellidea have also a very wide distribution, for the two species which at present compose the sub-order come from Davis Straits and from the Gulf of Siam, at depths of 1870 fathoms and of 1 fathom respectively.

The marine Gammaridea are rarely pelagic; they are abundant in the littoral region and penetrate to great depths. The vast abundance of individuals and species in Arctic and Antarctic seas is especially noteworthy. As regards the freshwater species, the predominance of the genus *Gammarus* and its nearest allies must

be noticed; the occurrence of species from genera otherwise marine in the "relict" faunas of lakes in Northern Europe and America and in the Caspian Sea; the peculiar blind subterranean species (*Niphargus*, etc.) which come to the surface in wells and penetrate into the abyssal waters of deep lakes; and the radiation of single genera into numerous species in a limited area in the *Gammari* of Lake Baikal and the *Hyalellae* of Lake Titicaca. The only terrestrial Amphipoda occur among the Talitridae, which in northern latitudes live, for the most part, just above tide-marks, but in the warmer regions of the globe penetrate inland to great distances.

Perhaps no Amphipoda except the whale-lice (Cyamidae) (Fig. 135) are truly parasitic, though some forms with suctorial mouth-parts seem to be semi-parasitic on fish (*Trischizostoma*). Many species, however, are commensal with sponges and other organisms. The pelagic *Phronima* (Fig. 136) lives in a transparent barrel-shaped case fashioned from the swimming-bell of a Siphonophore or from a test of a pelagic Tunicate.

The Gammaridea probably include the smallest as well as the largest Amphipoda, for many species do not exceed two or three millimetres in length. The largest is *Alicella gigantea*, Chevreux, which reaches a length of 140 mm.

Palaeontology.

Fossil remains of Amphipoda are exceedingly rare, and although various problematical fossils from Palaeozoic rocks have been referred to this group, it is only in the Tertiary and Post-Tertiary deposits that undoubted Amphipoda have been found. All belong to the Gammaridea, and though a genus *Palaeogammarus* has been established for a species found in Baltic amber, its generic and even specific distinctness from some of the living forms of *Gammarus* is uncertain.

Affinities and Classification.

Although the Amphipoda plainly belong to the Peracaridan division of the Malacostraca, their relation to the other Orders of the division is by no means so clear as in the case of the Isopoda. It seems very likely that their affinity to the Isopoda is not so close as has been supposed. Apart from the sessile eyes and the segmentation of the body, characters which, there is reason to suppose, have originated independently in at least one other case (*Koonunga*), almost the only point of agreement between the two Orders is found in the possession of coxal plates on the thoracic somites. But coxal plates are not developed in the most primitive Isopoda, the Asellota, and if their appearance in that Order was later than the acquisition of the typical Isopodan characters, the

coxal plates of the Amphipoda must have had an independent origin. The possession, by the typical Amphipoda, of a well-developed inner ramus on the antennule and of a palp on the maxillula are also among the characters which suggest that they diverged from the common stock before the origin of the Isopoda. It is quite probable, however, that their origin must be sought for still further back. They do not show the late appearance of the last thoracic limbs and the tendency to coalescence of the telson with the last somite—characters which are common to Cumacea, Tanaidacea, and Isopoda—while they possess a well-developed antennal gland, which is never more than vestigial in these Orders. Further, if the branchiae of the Amphipoda be, as Claus suggests, epipodites which have become shifted from the outer to the inner surface of the thoracic coxopodites, it follows that the Amphipoda must be supposed to have diverged, not later than the origin of the Mysidacea, from the primitive caridoid stock of the Peracarida.

A regards the four sub-orders recognised in the classification given below, it must be admitted that the differences separating the Gammaridea from the Caprellidea are not very profound. A Caprellid which should unite the abdomen of *Cercops* with the thoracic limbs of *Phtisica* would be very hard to exclude from the Gammaridea. The Hyperiidea hardly depart more widely from the Gammaridea, but the retention of the three divisions is at least convenient. The sub-order Ingolfiellidea, established by Hansen for the two species of the genus *Ingolfiella*, is not admitted by Stebbing, who places the genus among the Gammaridea, but there seems to be force in Hansen's contention that its inclusion in that sub-order would logically require the absorption of the Caprellidea also.

The difficulties in the way of classifying the Amphipoda are of a different order from those met with among the Isopoda. We have to deal with a vast diversity of forms within a comparatively small range of morphological variation, with the consequence that genera and even families have to be established on trivial characters, and their limits are often hard to define.

ORDER **Amphipoda**, Latreille (1816).

SUB-ORDER 1. **Gammaridea**, Dana (1852).

Head not coalesced with second thoracic somite; palp of maxillipeds with two to four segments; all the thoracic legs present, usually with well-developed coxal plates; abdominal somites generally distinct, with well-developed appendages; eyes rarely very large.

Family LYSIANASSIDAE. *Lysianassa*, H. Milne-Edwards; *Alicella*,

Chevreux; *Socarnes*, Boeck; *Trischizostoma*, Boeck. Family STEGOCEPHALIDAE. *Stegocephalus*, Kroyer. Family AMPELISCIDAE. *Ampelisca*, Kroyer. Family HAUSTORIIDAE. *Haustorius*, S. Muller; *Urothoe*, Dana. Family PHOXOCEPHALIDAE. *Phoxocephalus*, Stebbing. Family AMPHILOCHIDAE. *Amphilochus*, Spence Bate. Family LEUCOTHOIDAE. *Leucothoe*, Leach. Family ANAMIXIDAE. *Anamixis*, Stebbing. Family METOPIDAE. *Metopa*, Boeck. Family CRESSIDAE. *Cressa*, Boeck. Family STENOTHOIDAE. *Stenothoe*, Dana. Family PHLIANTIDAE. *Phlias*, Guérin; *Pereionotus*, Spence Bate and Westwood. Family COLOMASTIGIDAE. *Colomastix*, Grube. Family LAFYSTIIDAE. *Lafystius*, Kroyer. Family LAPHYSTIOPSIDAE. *Laphystiopsis*, G. O. Sars. Family ACANTHONOTOZOMATIDAE. *Acanthonotozoma*, Boeck. Family PARDALISCIDAE. *Pardalisca*, Kroyer. Family LILLJEBORGIIDAE. *Lilljeborgia*, Spence Bate. Family OEDICEROTIDAE. *Oediceros*, Kroyer. Family SYNOPIIDAE. *Synopia*, Dana. Family TIRONIDAE. *Tiron*, Lilljeborg. Family CALLIOPIIDAE. *Calliopius*, Lilljeborg. Family PLEUSTIDAE. *Pleustes*, Spence Bate. Family PARAMPHITHOIDAE. *Paramphithoe*, Bruzelius. Family ATYLIDAE. *Atylus*, Leach. Family MELPHIDIPPIDAE. *Melphidippa*, Boeck. Family EUSIRIDAE. *Eusirus*, Kröyer. Family BATEIDAE. *Batea*, F. Muller. Family PONTOGENEIIDAE. *Pontogeneia*, Boeck. Family GAMMARIDAE. *Gammarus*, Fabricius (Fig. 132); *Niphargus*, Schiodte; *Synurella*, Wrzesniowski; *Melita*, Leach. Family DEXAMINIDAE. *Dexamine*, Leach; *Polycheria*, Haswell. Family TALITRIDAE (ORCHESTIIDAE). *Talitrus*, Latreille; *Orchestia*, Leach; *Hyalella*, S. Smith. Family AORIDAE. *Aora*, Kroyer. Family PHOTIDAE. *Photis*, Kroyer. Family ISAEIDAE. *Isaea*, H. Milne-Edwards. Family AMPHITHOIDAE. *Amphithoe*, Leach. Family JASSIDAE (PODOCERIDAE auctt.). *Jassa*, Leach (*Podocerus* auctt.). Family COROPHIIDAE. *Corophium*, Latreille. Family CHELURIDAE. *Chelura*, Philippi. Family PODOCERIDAE. *Podocerus*, Leach (= *Platophium*, Dana). Family HYPERIOPSIDAE. *Hyperiopsis*, G. O. Sars.

SUB-ORDER 2. **Hyperiidea**, Dana (1852).

Head not coalesced with second thoracic somite; palp of maxillipeds absent; all the thoracic legs present, coxopodites small or coalesced with the body; abdominal somites generally distinct, with well-developed appendages; eyes generally very large.

Family SCINIDAE. *Scina*, Prestandrea. Family VIBILIIDAE. *Vibilia*, H. Milne-Edwards. Family CYLLOPODIDAE. *Cyllopus*, Dana. Family LANCEOLIDAE. *Lanceola*, Say. Family CYSTISOMATIDAE. *Cystisoma*, Guérin. Family PARAPHRONIMIDAE. *Paraphronima*, Claus. Family PHRONIMIDAE. *Phronima*, Latreille (Fig 136). Family MIMONECTIDAE. *Mimonectes*, Bovallius. Family HYPERIIDAE. *Hyperia*, Latreille; *Phronimopsis*, Claus; *Euthemisto*, Bovallius. Family PHROSINIDAE. *Phrosina*, Risso. Family PHORCORRHAPHIDAE. *Phorcorrhaphis*, Stebbing. Family PLATYSCELIDAE. *Platyscelus*, Spence Bate. Family SCELIDAE. *Thyropus*, Dana. Family PRONOIDAE. *Pronoe*, Guérin. Family TRYPHANIDAE. *Tryphana*, Boeck. Family OXYCEPHALIDAE. *Oxycephalus*, H. Milne-Edwards; *Rhabdosoma*, White (Fig. 133).

SUB-ORDER 3. **Caprellidea**, Dana (1852).

Head coalesced with second thoracic somite; palp of maxillipeds with from one to four segments (rarely absent); rarely all the thoracic legs well developed, fourth and fifth pairs usually vestigial or absent, coxopodites small or coalesced with the body; abdominal somites generally all fused, appendages vestigial; eyes small.

Family CAPRELLIDAE. *Cercops*, Kroyer; *Phtisica*, Slabber (*Proto*, Leach) (Fig. 134, A); *Caprella*, Lamarck (Fig. 134, B). Family CYAMIDAE. *Cyamus*, Latreille; *Platycyamus*, Lutken; *Paracyamus*, G. O. Sars (Fig. 135).

SUB-ORDER 4. **Ingolfiellidea**, Hansen (1903).

Head not coalesced with second thoracic somite; palp of maxillipeds with four segments; all the thoracic legs present, coxopodites small; abdominal somites distinct, first three and last pairs of abdominal appendages vestigial; eyes wanting but articulated eye-lobes are present.

Family INGOLFIELLIDAE. *Ingolfiella*, Hansen.

LITERATURE.

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CHAPTER XIV

THE EUPHAUSIACEA

Order **Euphausiacea**, Boas (1883).

Definition.—Eucarida which retain the primitive caridoid facies; the exopodite of the maxilla is small; none of the thoracic limbs are specialised as maxillipeds; branchiae in a single series, attached to the coxopodites of the thoracic limbs (podobranchiae); young hatched in the nauplius-stage.

Historical.—The genus *Thysanopoda* was placed by H. Milne-Edwards in his tribe of "Mysiens," and most subsequent writers have retained the association of Euphausiacea and Mysidacea in the group "Schizopoda." As already mentioned, Boas was the first to separate the two orders. Some of the later larval stages were described as distinct genera by Dana before their true nature was pointed out by Claus. Metschnikoff's discovery of the nauplius stage of *Euphausia* (1869) drew special attention to the larval history of the group. The most complete account of the structure, development, and classification of the Order is that given by G. O. Sars in his "Challenger" Report. The phosphorescence of certain Euphausians was first observed by J. V. Thompson; the light-producing organs have been investigated by several zoologists, the most detailed account being that given by Chun.

MORPHOLOGY.

The general form of the body (Fig. 139) is completely caridoid. The carapace coalesces dorsally with all the thoracic somites, and is produced in front as a rostrum which is never of great length.

The telson (Fig. 142, C) has a pair of large movably articulated spines (*s*) near the tip. Sars has shown that these are formed by enlargement of one out of several pairs of marginal setae which are present in the larvae, and it is therefore impossible to regard them as representing the caudal furca of the Leptostraca.

Appendages.—The *antennules* are always biramous, and some-

times show sexual modifications in the male. The *antennae* have a protopodite of two segments, a large lamellar scale or exopodite, and an endopodite with three peduncular segments and a long

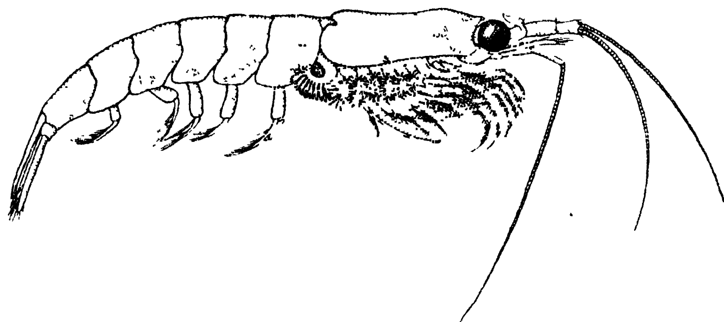


Fig. 139.
Meganyctiphanes norvegica, ♂, × 2.

flagellum. The *mandibles* (Fig. 140, A) generally have a palp; the incisor process is directly connected with the molar process, there being no lacinia mobilis or row of spines in the adult,

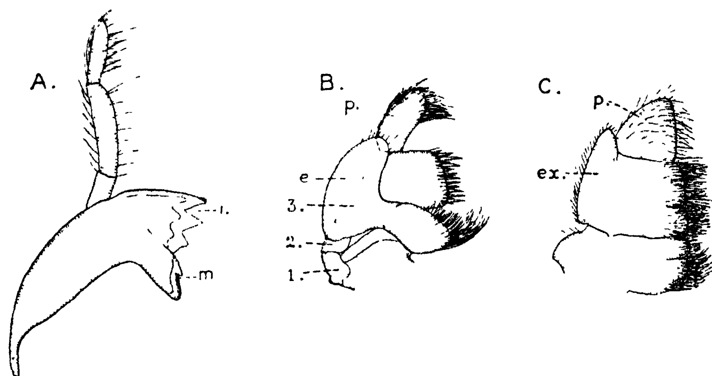


Fig. 140.
Mouth-parts of *Meganyctiphanes norvegica*. A, mandible; B, maxillula; C, maxilla. *e*, exite of first segment of maxillula; *ex*, exopodite of maxilla; *i*, incisor process; *m*, molar process; *p*, palp.

although some spines are present in the larval stages. The *maxillulae* (Fig. 140, B) have the usual two endites and a palp which is generally unsegmented, but has three segments in *Bentheuphausia* and two in some larvae. An exite of the third segment (exopodite) is present in the larva, but is replaced in the adult by an exite (*e*) of the first segment, sometimes erroneously called

of eleven pairs of ganglia can be distinguished, all of them, however, united in a common sheath of connective tissue. The paired eyes are each divided into two parts in the sub-family Nematoscelinae, the fronto-dorsal division having elongated ommatidia of a structure supposed to be adapted for perception of very faint light. The nauplius-eye persists in the adult, lying between the paired eyes beneath the rostrum.

No statocysts have been found in any Euphausiacea. A system of very remarkable organs, formerly regarded as "accessory eyes" but now known to be luminous organs (photospheres), is found in all Euphausiacea except *Bentheuphausia*. As a rule, two pairs of these organs are situated in the coxopodites of the second and seventh pairs of thoracic appendages respectively (Fig. 141, *p*), an unpaired series on the sternal surface of the abdomen between the bases of each of the first four pairs of pleopods, and a pair, differing in structure from the others, on the upper surfaces of the ocular peduncles. In *Stylocheiron*, only the posterior thoracic pair, the first abdominal organ, and those on the ocular peduncles are present. Each of the thoracic and abdominal photospheres (Fig. 143) is globular in form, lying beneath and detached from the hypodermis, and, in some cases at least, moved by special muscles. The centre of the organ is occupied by a "striated body" (*str*) composed of radiating lamellae, which seems to be the actual source of light, and in which the fibrils of a special nerve appear to terminate. On the inner side of the photosphere is a concave reflector (*r*) composed of concentric lamellae, and on the outer side is a lens (*l*), the whole surrounded, except on the outer side, by a sheath of pigment (*pg*). The organs on the ocular peduncles differ in the absence of a lens, in their incomplete separation from the hypodermis, and in other details of structure.

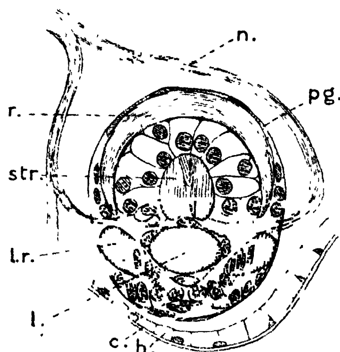


FIG. 143.

Section through one of the thoracic phosphorescent organs of *Nematoscelis*. *c*, cuticle; *h*, hypodermis; *l*, lens; *l.r.* ring of lamellae surrounding the lens; *n*, nerve; *pg*, pigment; *r*, reflector; *str*, striated body. (After Chun.)

The spermatozoa are simple round or oval nucleated cells. They are transferred to the female in lageniform spermatophores, which are formed within the widened terminal parts of the vasa deferentia.

The ova are small in size and are sometimes carried, probably only for a short time, "loose among the thoracic legs, which, with their setae, form a sort of basket" (Holt and Tattersall, *Euphausia*).

In other cases the ova are agglutinated together in a paired or unpaired mass, which is carried attached to the sternal surface of the thorax, close to the bases of the posterior thoracic legs. These egg-packets are formed by some cementing material apparently extruded along with the eggs, and bear no sort of morphological resemblance to the brood-sac of the Mysidacea which is formed by the oostegites.

Development.

With the possible exception of the genus *Stylocheiron*, where the relatively large size of the eggs suggests an abbreviated metamorphosis, the Euphausiacea leave the egg in the form of a typical nauplius, and reach the adult stage by a series of changes closely parallel to those occurring in the metamorphosis of the Penaeidea among the Decapoda. Claus was the first to show that the forms described by Dana as distinct genera under the names *Calyptopis*, *Furcilia*, and *Cyrtopia* are successive stages in the development of Euphausiacea, and Sars has been able to fill in, with considerable detail for several species, the outline thus furnished.

The newly hatched nauplius, as described by Metschnikoff and by Sars, has an oval unsegmented body, without shell-fold, and with the three pairs of nauplius appendages in their typical form, the first uniramous, the second and third biramous; the median eye is not developed till the next stage. The mouth is not at first open, and there is no masticatory process on the base of the antenna such as exists in Copepoda and Cirripedia.

In the next stage the larva assumes the form of a metanauplius (Fig. 144, A), showing rudiments of three additional pairs of appendages, maxillulae, maxillae, and first thoracic limbs; the shell-fold is defined posteriorly and partly envelops the hinder end of the body. In later metanauplius-stages the third pair of appendages (mandibles) lose their natatory character and become reduced to the basal masticatory part, with only a very small rudiment to represent the palp; the shell-fold now projects in front as well as behind and overhangs the head in a hood-like form.

The metanauplius is succeeded by a series of *Calyptopis*-stages (Fig. 144, B, C) characterised by the elongation of the trunk-region and the differentiation of its somites in regular order from before backwards. The thoracic somites are very short and crowded together. The appendages already present become more fully developed, and, later, the rudiments of the last pair of abdominal appendages appear. The paired eyes develop but are covered at this stage by the frontal hood of the carapace.

In the next succeeding *Furcilia*-stages the paired eyes become free and movable. The pleopods develop from before backwards and, later, the anterior thoracic limbs. The *Cyrtopia*-stage is

characterised chiefly by changes in the antennules and antennae. The former, which have become biramous already in the *Calyptopis*-stage, now elongate, while the latter lose their natatory function, and their rami, at first similar, become differentiated into "scale" and flagellum respectively. The *Cyrtopia* gradually assumes the form

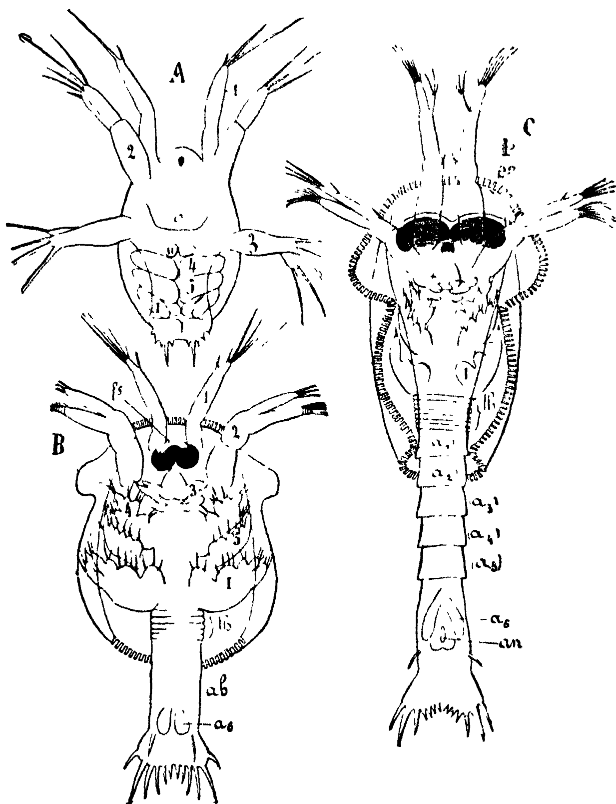


Fig. 144.

Larval stages of *Euphausia*. A, metanauplius. B, calyptopis. C, later calyptopis-stage. 1, antennule; 2, antenna; 3, mandible; 4, maxillula; 5, maxilla; I, first thoracic appendage; *th*, thoracic somites; *ab*, abdomen; (a_1)-(a_5), first five abdominal somites; a_6, uropod; *an*, anus; *f.s*, frontal sense-organs. (A after Metschnikoff; B and C after Claus; from Korschelt and Heider's *Embryology*.)

of the adult by the successive development of the remaining thoracic limbs.

The development of the various appendages, which has been traced in detail by Sars, offers many features of interest. The palp of the mandible only begins to redevelop in the *Cyrtopia*-stage. The maxillula has at first a small lobe on its outer edge which appears to represent the exopod and is quite independent of the

plate which in the adult has been regarded as the exopod, but which is in reality a process of the first segment of the limb. A very remarkable feature in the development of the paired eyes has been found by Sars in the case of *Nematoscelis*. Here, a transitory larval eye consisting of seven ommatidia is formed at the apex of the eye-stalk and is later pushed to the outer side by the development of the permanent visual organ. Though this transitory organ is stated to disappear in the adult, it seems possible that it may really persist as the luminous organ of the eye-stalk, especially since in other genera (*Nyctiphanes*, *Euphausia*) the luminous organ appears before the eye itself. The heart is visible already in the later metanauplius-stages. The liver at first consists of three caecal tubes on each side.

Remarks on Habits, etc.

The Euphausiacea are characteristically pelagic animals, forming part of the surface-plankton of the ocean and descending to considerable depths. They are generally remarkably transparent, but *Bentheuphausia*, which appears to be a true deep-sea form (1000-1800 fathoms), is said to be "quite opaque and of a similar vivid red colour to that of most other true deep-sea crustaceans." The adult size of most Euphausiacea lies between 10 and 40 mm.; a species of *Thysanopoda* reaches 55 mm. in length.

No fossil Euphausiacea are known.

Affinities and Classification.

The differences in structure which justify the separation of the Euphausiacea from the Mysidacea have already been insisted on. A certain degree of resemblance in general facies is sufficiently accounted for, on the one hand, by the approximation of the basal members of the Peracaridan and Eucaridan lines of descent to the common caridoid stock of the Eumalacostraca; and on the other, by the similarity in habitat between the Euphausiacea and many of Mysidacea. The resemblances between the members of the present Order and some of the lower Decapods, especially the Penaeidea, are of much greater importance. The complex copulatory armature of the first pleopods has a general resemblance to that of the Penaeidea, the larval development of the two groups is closely parallel, and the presence in some Sergestidae of phosphorescent organs resembling, though differing in details from, those of the Euphausiacea may also be an indication of affinity.

At present, the Euphausiacea are regarded as constituting only a single family.

ORDER **Euphausiacea**, Boas (1883).

Family EUPHAUSIIDAE. Sub-Family EUPHAUSIINAE. *Euphausia*, Dana; *Thysanopoda*, Milne-Edwards; *Nyctiphanes*, G. O. Sars; *Meganyctiphanes*, Holt and Tattersall (Fig. 139). Sub-Family NEMATOSCELINAE. *Nematoscelis*, G. O. Sars; *Nematobrachion*, Calman; *Stylocheiron*, G. O. Sars. Sub-Family BENTHEUPHAUSIINAE. *Bentheuphausia*, G. O. Sars.

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CHAPTER XV

THE DECAPODA

Order **Decapoda**, Latreille (1802).
Sub-Order 1. **Natantia**.
Tribe 1. PENAEIDEA.
" 2. CARIDEA.
" 3. STENOPIDEA.
Sub-Order 2. **Reptantia**.
Section 1. PALINURA.
Tribe 1. ERYONIDEA.
" 2. SCYLLARIDEA.
Section 2. ASTACURA.
Tribe NEPHROPSIDEA.
Section 3. ANOMURA.
Tribe 1. GALATHEIDEA.
" 2. THALASSINIDEA.
" 3. PAGURIDEA.
" 4. HIPPIDEA.
Section 4. BRACHYURA.
Tribe 1. DROMIACEA.
Sub-Tribe 1. DROMIIDEA.
" 2. HOMOLIDEA.
Tribe 2. OXYSTOMATA.
" 3. BRACHYGNATHA.
Sub-Tribe 1. BRACHYRHYNCHA.
" 2. OXYRHYNCHA.

Definition.—Eucarida in which the caridoid facies may be retained or may be greatly modified; the exopodite of the maxilla is very large (scaphognathite); the first three pairs of thoracic limbs are specialised as maxillipeds; branchiae typically in several series, attached to the coxopodites of the thoracic limbs (podobranchiae), to the articular membranes (arthrobranchiae), and to the

lateral walls of the thoracic somites (pleurobranchiae), very rarely absent; young rarely hatched in nauplius-stage.

Historical.—The great majority of the larger and more familiar Crustacea belong to the Decapoda, and this Order received far more attention from the older naturalists than any of the others. A considerable number of species are mentioned by Aristotle, who describes various points of their anatomy and habits with accuracy, and sometimes with surprising detail. A long series of purely descriptive writers who have added to the number of known forms without contributing much to a scientific knowledge of them begins with Belon and Rondelet in the sixteenth century, and perhaps does not altogether come to an end with Herbst's *Naturgeschichte der Krabben und Krebse* (1782-1804). Among the most noteworthy of early contributions to anatomy are Swammerdam's memoir on the Hermit-Crab (1737), and that of Roesel von Rosenhof on the Crayfish (1755). Réaumur's observations on the phenomena of ecdysis and the regeneration of lost parts in the Crayfish (1712-1718) have become classical. The foundations of classification were laid by J. C. Fabricius (1793), who divided the Linnean genus *Cancer* into a large number of genera, the majority of which are still recognised. Latreille, to whom the name of the Order is due (1802), also began its subdivision into sub-orders and families. In this more than in any other group of Crustacea the works of H. Milne-Edwards, and especially his *Histoire Naturelle des Crustacés*, may be taken as marking the beginning of the modern period, and his classification of the Decapoda has been that most generally accepted until very recently. Almost contemporaneous with Milne-Edwards's great work, and often surpassing it in morphological detail and systematic insight, was de Haan's volume on the Crustacea of Japan (1833-1849). The first important departure from the general plan of classification laid down by these authors was made by Boas in 1880, and his system has been further elaborated by Ortmann and by Borradaile. J. Vaughan Thompson's discovery of the larval metamorphosis of Decapoda (1828-1831), confirming the earlier observations of Slabber and Cavolini in the eighteenth century, gave rise to a curious controversy in which Westwood and others denied the possibility of such a metamorphosis, basing their arguments chiefly on Rathke's memoir on the development of the Crayfish (1829). F. Müller in 1863 made the highly important discovery that *Penaeus* is hatched from the egg in the form of a nauplius, and the clue thus given to the interpretation of the other larval stages was followed up especially by Claus. The development of deep-sea exploration within the last thirty years has resulted in the discovery of a large number of important new types of Decapoda, which have been described by Spence Bate, Miers, Henderson, A. Milne-Edwards, Bouvier, Faxon, Alcock, and others. The numerous

species of fossil Decapoda have been little studied from the point of view of phylogeny, but reference may be made to Bouvier's essay on the origin of the Brachyura as an example of the results which may be obtained in this department. Among other papers which have been fruitful in suggesting lines of research for later workers may be mentioned Huxley's memoir on the classification and distribution of the Crayfishes (1878); A. Milne-Edwards's note on the transformation of the ocular peduncle into an antenna-like organ in a Palinurid (1864), the forerunner of much recent work on regeneration and abnormalities; Giard's papers on parasitic castration; and Faxon's discovery of the alternating dimorphism in the males of *Cambarus*.

Morphology.

Amid the great diversity of general shape exhibited by the Decapoda, two chief types may be distinguished. In the first or Macrurous type the general caridoid facies is retained, the body is elongated and subcylindrical, the abdomen is long and terminates in a tail-fan. In the Brachyurous type (which is not confined to the Brachyura, but recurs in several groups of Anomura) the cephalothorax is greatly expanded laterally and more or less depressed, while the abdomen is reduced and folded underneath the cephalothorax. A very peculiar modification is found in most Paguridea, where the abdomen is markedly asymmetrical and spirally coiled, in correlation with the habit of living in the empty shells of Gasteropod Molluscs.

The carapace coalesces dorsally with all the thoracic somites and overhangs on each side as a *branchiostegite*, enclosing the branchial chamber within which the gills are concealed. Anteriorly it may be produced into a rostrum, which in a few genera of Caridea (*Rhynchocinetes*, etc.) is movably articulated. In most Brachyura the rostrum is reduced to a short but broad frontal plate, of which the relations to the adjacent parts will be described below. In some Macrura (Scyllaridae) and in many Anomura and Brachyura, where the cephalothorax is flattened from above downwards, the lateral portions of the carapace are abruptly bent inwards towards the bases of the legs. The lateral margin thus produced is commonly toothed or otherwise armed.

The surface of the carapace is commonly marked by depressions and grooves corresponding in part to the insertions of various muscles, but in part independent of these. In this way several regions of the carapace are defined which, especially in the Brachyura, may be still further divided into sub-regions. For convenience of systematic description these various areas are denominated according to a scheme of terminology introduced for the most part by H. Milne-Edwards (1851). More recently the furrows of the

carapace have been studied by Boas and by Bouvier. Only a few points can be mentioned here. In the lobsters and crayfish a conspicuous groove (Fig. 145, *c*) crosses the dorsal surface of the carapace transversely about the middle of its length and curves forwards on either side. This groove, named the "cervical groove" by Milne-Edwards (*c* in Boas's terminology, the "branchial groove" of Bouvier), was supposed by him to indicate the line of division between the portions of the carapace arising from the antennal and mandibular somites respectively. Other writers, for instance, Huxley, regarded it as marking the limits of the cephalic and thoracic regions. There appears to be no ground, however, for regarding this groove as of greater importance than some of the other grooves of the carapace. In some cases an equally conspicuous transverse groove (*e* of Boas, "cervical groove" of Bouvier) (Fig. 145, *e*, *e'*) crosses the carapace a little in front of the cervical, and as this is the only transverse groove, apparently, to be found in any of the lower Macrura (Stenopidea, Caridea), it seems at least as likely to afford an important morphological landmark. In some cases portions of the carapace may be separated by a longitudinal groove or uncalcified line, which may even form a movable hinge. Of this nature are the *linea thalassinica* (Fig. 146, *l.t*) of the Thalassinidea, with which the *l. homolica* of the Homolidae may perhaps be identical, and the *l. anomurica* (*l.a*) of many Anomura, identified with the *l. dromiidica* of Dromiidae and the unfortunately named "epimeral suture" of other Brachyura.

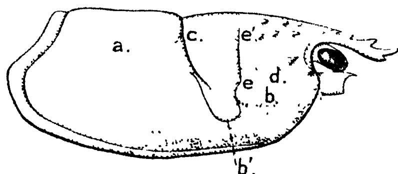


Fig. 145.

Carapace of the Norway Lobster (*Nephrops norvegicus*) from the side. (After Boas.) The letters referring to the grooves of the carapace are those used by Boas. *e*, *e'*, the "cervical groove" of Bouvier, "anterior cervical groove" of Borradaile; *c*, "branchial groove" of Bouvier, "posterior cervical groove" of Borradaile.

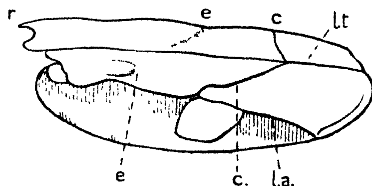


Fig. 146.

Carapace of *Callianassa novaebritanniae* (Thalassinidea) from the left side. (After Borradaile.) *c*, *e*, the grooves so lettered by Boas (see Fig. 144); *l.a*, *linea anomurica* (perhaps also the *linea dromiidica*), the front part of which is the line *b* of Boas; *l.t*, *linea thalassinica* (perhaps also the *linea homolica*), the front part of which is the line *d* of Boas; *r*, rostrum.

The sternal surface of the cephalothorax is very narrow in many Macrura, but is often broad in those which have a depressed form. It is broad in many Anomura and in all Brachyura, with the exception of Raninidae. The thoracic sterna are usually clearly distinguishable, and, in the lower forms, seem to preserve a certain

degree of mobility. In the higher forms they become firmly united, with the exception of the last thoracic sternum, which may be movable (Astacidae, Parastacidae, and Anomura).

In front of the mouth, regions representing the sterna of the three preoral "somites" can be distinguished, but on account of the "cephalic flexure" the ophthalmic and antennular sterna are directed forwards, or even upwards. The antennal sternum is mainly represented by the *epistome*, a plate of varying shape lying between the labrum and the bases of the antennae. In the Natantia the epistome is comparatively narrow, and on each side is separated from the lateral portions of the carapace by the exhalent branchial channels. In most of the Reptantia the epistome (Fig. 147, A, *ep*) is broad and comes in contact with the carapace on each side, and in the Brachyura it becomes firmly united with it. In this way there is defined more or less distinctly a *buccal frame* within which lie the mouth-parts, and which in most Brachyura is closed by the operculiform third maxillipeds. The sides of this buccal frame are formed by the free antero-lateral margins of the carapace (Fig. 147, B, *l.m*), while in front it is more or less distinctly delimited by the epistome itself, or by a transverse ridge (Fig. 147, B, *a.m*) which divides the epistome into two parts, the epistome proper and the *endostome* or palate (*end*). In most Brachyura also (except the Dromiacea) the proximal segments of the antennae are fused with the epistome. In the Macrura the anterior margin of the carapace forms on each side of the base of the rostrum a more or less distinct "orbital notch," within which the eye rests when it is turned outwards. In the Brachyura this transverse direction of the eye-stalks is permanent, and the orbit is usually (except in Dromiacae) completed by the downgrowth of a process (*l.p*) from the front, external to the antennules, which unites either directly or, more usually, by intervention of the second segment of the antenna, with the sub-orbital lobe (*s.o*) of the carapace. Further, in all the Brachyura the rostrum or frontal plate sends downwards in the middle line a process (*m.p*) which unites in front of the ophthalmic and antennular sterna with the epistome, and separates from one another the basal segments of the antennules. The greater part of the ophthalmic peduncle is in this way concealed in a kind of sheath, and only the terminal segment appears and is movable within the orbit.

In the Dromiacea the second segment of the antennal peduncle is free and there is no corresponding process of the front, so that the orbits are incompletely or not at all defined. The arrangement is hardly more complete in certain Oxyrhyncha (*Macrocheira*) (Fig. 147, B), but in most Brachyura the antennal peduncle joins with the front to form a partition separating completely the orbits from the "antennular fossae," into which the antennules

may be withdrawn. There is, however, great diversity in the details of structure of the "facial" region among the Brachyura, and these are of considerable value as systematic characters.

In the Scyllaridae among the Macrurous groups the cephalic

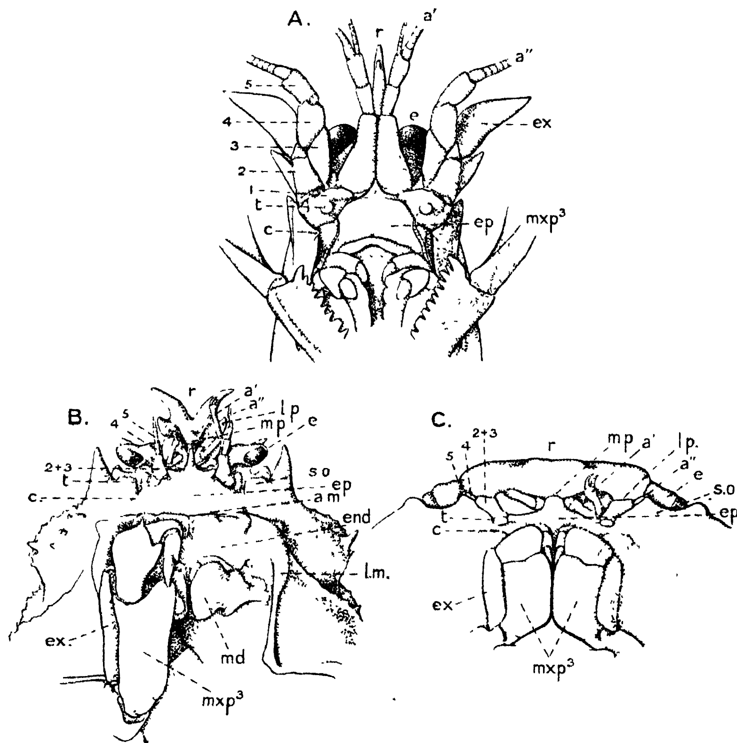


FIG. 147.

Head and anterior part of body from below. A, *Nephrops norvegicus*. B, *Macrocheira Kaempferi*. C, *Carpilius convexus*. (Drawn by Miss G. M. Woodward.) *a'*, antennule; *a"*, antenna; *a.m*, ridge forming anterior margin of the mouth-frame and dividing the epistomial area into epistome proper and endostome; *c*, point where the lateral wing of the carapace touches, or, in B and C, fuses with, the epistome; *e*, eye, in C retracted into, and partly concealed by, the orbit; *end*, endostome; *ep*, epistome; *ex*, exopodite; *l.m*, lateral margin of buccal frame; *l.p*, lateral process of rostral plate, which in C comes in contact with the basal segment (2+3) of the antenna; *md*, mandible; *mp*, median process of the front (in B and C) uniting with anterior process of epistome; *mxp*3, third maxilliped; *r*, rostrum or (in C) frontal plate; *s.o*, suborbital lobe forming floor of orbit; *t*, in A, tubercle bearing opening of antennal gland, in B and C, operculum covering the opening and probably representing the reduced first segment of the antenna; 1-5, the segments of the antennal peduncle.

region is modified in a way that at first sight suggests the Brachyurous type, the eyes being widely separated and lodged in complete orbits. In this case, however, the front unites in the middle line not with the epistome but with the greatly enlarged antennular somite.

In the Alpheidae (Caridea) the anterior margin of the carapace

is modified in a very peculiar manner, growing over and, in most cases, completely enclosing the eyes.

The differences in the development of the abdominal region are no less conspicuous than in the case of the cephalothorax, and have been utilised as affording characters for the primary subdivisions of the Order. In the Natantia the abdomen is large and, with its appendages, forms the chief organ of swimming. It is generally more or less compressed and its somites have well-developed pleura. It is dorsally humped or bent between the third and fourth somites in many Caridea (Eukyphotes, Boas) (Fig. 148), but the character is not so constant as to justify great

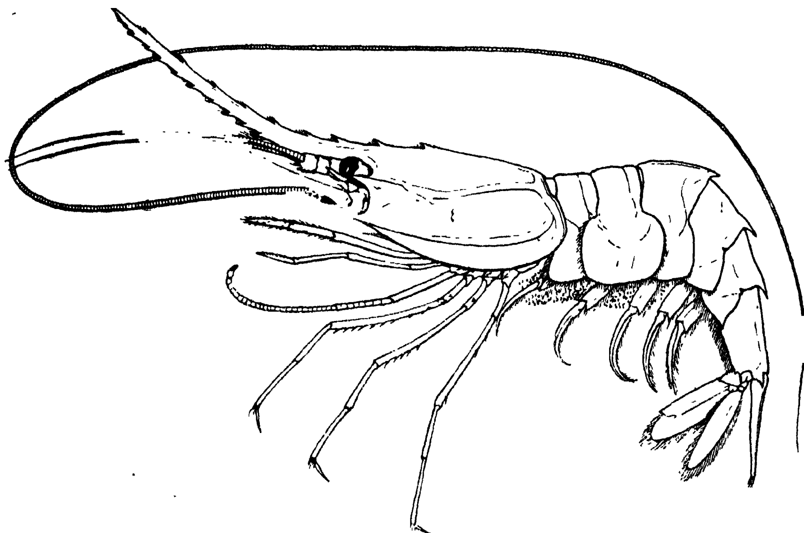


FIG. 148.

Heterocarpus Alphonsi (Caridea, Pandalidae), showing the "humped" form of the abdomen and the multiarticulate meropodite and carpopodite of the second leg. (From Alcock, *Naturalist in Indian Seas*.)

systematic importance being attached to it. In the Palinura and Astacura the importance of the abdominal appendages as natatory organs is generally reduced, and the abdomen itself is not humped.

Among the Anomura, the Thalassinidea (Fig. 149) have retained the extended abdomen of the Macrurous groups, but the pleura are more or less reduced; the Galatheidea (Fig. 150) have the abdomen more or less closely flexed under the cephalothorax but not greatly modified; the Paguridea, with the exception of some interesting transitional forms (Pylochelidae) (Fig. 151), have the abdomen and its appendages more or less unsymmetrically developed and its somites imperfectly indicated. In the hermit-crabs (Paguridae and Coenobitidae) the abdomen is soft-skinned and spirally

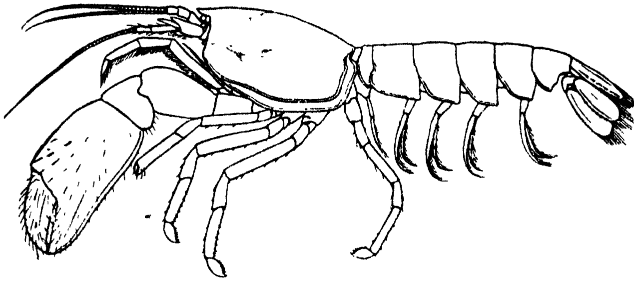


Fig. 149.

Iconaxiopsis andamanensis (Thalassinidea). (From Alcock, *Naturalist in Indian Seas.*)

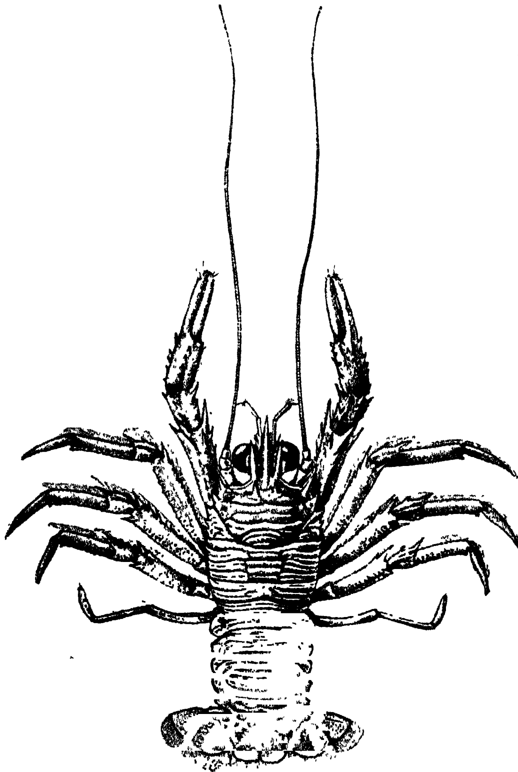


Fig. 150.

Munida andamanica (Galatheidae), abdomen extended. (From Alcock, *Naturalist in Indian Seas.*)

coiled to fit into the Gasteropod shells inhabited by the animals. Only the sixth somite and the telson are fully calcified, the tergal portions of the other somites being merely indicated by widely

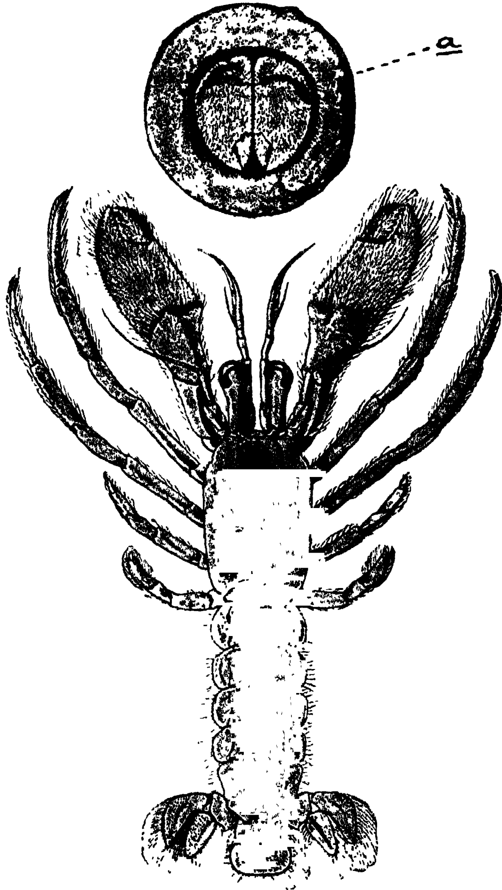


FIG. 151.

Pylocheles Miersii (Paguridea). *a*, end view of the animal lodged in a tube of water-logged mangrove or bamboo, its chelipeds closing the opening. The lower figure shows the animal in a conventional attitude after removal from its refuge. (From Alcock, *Naturalist in Indian Seas*.)

separated chitinous plates in the membranous investment of the dorsal surface. In the coco-nut crab *Birgus* (Coenobitidae) (Fig. 152), which has abandoned the use of a covering for the hinder part of the body, the abdomen, though short, is symmetrical and its terga are well calcified. In the Lithodidae (Fig. 153),

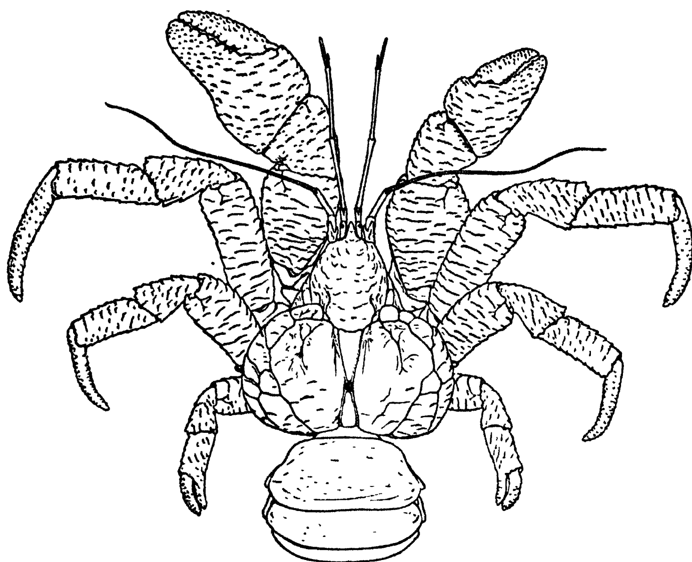


Fig. 152.

Birgus latro, ♂, about $\frac{1}{4}$th natural size. The last pair of thoracic legs are folded out of sight in the branchial chambers. (From Alcock, *Naturalist in Indian Seas.*)

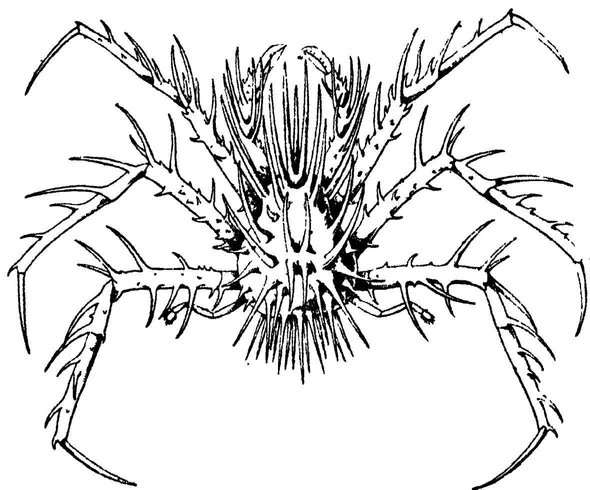


Fig. 153.

Neolithodes grimaldii (Lithodidae). (After Milne-Edwards and Bouvier, from *Ency. Brit.*)

which afford a remarkable instance of "convergence" in the assumption of the Brachyuran facies, the relationship to the hermit-crabs is shown by the fact that the short abdomen, which is closely bent up under the cephalothorax, has the terga incompletely calcified, and is, in the female, more or less unsymmetrical, bearing appendages only on one side.

Among the Brachyura the abdomen is always closely flexed under the cephalothorax, and is much reduced in size. The shape usually differs much in the two sexes, being narrow in the male but broad and often excavated for the reception of the eggs in the female. The terga of all the six somites, as well as the telson, may remain distinct, but very often two or three of the somites may become coalesced, especially in the male sex.

In the region of the thorax a system of internal skeletal structures is developed by infoldings of the cuticle (apodemes) forming the *endophragmal system.* In the Natantia, with feebly calcified integument, this system is but slightly developed, but in the Palinura and Astacura, and especially in the Brachyura, it attains a great degree of complexity. A "sternal canal" may be formed by the meeting of the sternal apodemes of opposite sides above the nerve-cord, and in the anterior part of the thorax this may give a firm plate or "entosternite" lying between the nerve-cord and the alimentary canal. It is not certain whether this entosternite involves any elements other than those supplied by the ectodermal and cuticular infoldings forming the apodemes; if it does not it can hardly be regarded as homologous with the entosternite already mentioned in Branchiopoda (p. 44), which appears to be of mesodermal origin.

In the Brachyura a sternal canal is not formed, the union of the apodemes being confined to one or two of the posterior thoracic somites, where it gives rise to a transverse bar known as the "sella turcica."

Appendages.—Among the Decapoda the *ocular peduncles* (Fig. 154) assume more the character of limbs than they do in any other Crustacea, since they are generally (perhaps always) divided into two, or more rarely three, movable segments. Instances of extreme development of the eye-stalks occur among Caridea and Brachyura, sometimes the first (*Podophthalmus*, Fig. 154, C) and sometimes the second segment (*Macrophthalmus*, Fig. 154, D) being elongated. The corneal surface is generally terminal, but may be oblique and even lateral, the peduncle running out beyond it into a styliform process which may equal in length the rest of the eyestalk (*Ocypoda*, Fig. 155). In certain species of *Gelasimus* one of the ocular peduncles terminates in a long process of this kind while the other does not. In cases where the eyes are atrophied, as in abyssal or cavernicolous decapods, the peduncle often persists in a reduced state (Figs. 161, 162).

The *antennules* have the three segments of the peduncle always distinct, and as a rule both flagella are present. In many Caridea

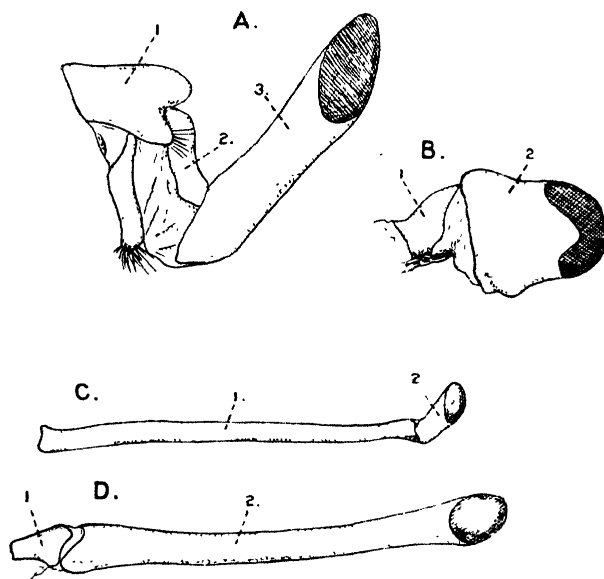


Fig. 154.

Ocular peduncles of Decapoda. A. *Ranina scabra* (Brachyura). B. *Astacus fluviatilis* (Astacura). C, *Podophthalmus vigil* (Brachyura). D, *Macrophthalmus pectinipes* (Brachyura). 1, 2, 3, successive segments of the peduncle.



Fig. 155.

Ocypoda macrocera (Brachyura) in a natural attitude with the eyes elevated, showing the styliform prolongation of the ocular peduncles. (From Alcock, *Naturalist in Indian Seas*.)

(Fig. 156, A) the outer flagellum is bifurcated near the base, and in some cases the three flagella appear to arise separately from the

end of the peduncle. The proximal segment of the peduncle, which in most cases lodges the statocyst, possesses in the Natantia a very characteristic expansion of its outer margin in the form of a rounded lobe or spiniform process known as the *stylocerite* (*sty*). In the Brachyura the flagella are very short or quite vestigial; the basal segment is enlarged and generally firmly fixed in the antennular fossa, and the other two segments fold up beside it.

Certain special modifications of the antennules may be mentioned here. In the Sergestidae the outer flagellum of the male is bifurcated and forms apparently a prehensile organ. In *Hymenocera* (Caridea) the inner flagellum is broadly foliaceous. In *Solenocera* (Penaeidae) the same flagellum is in the form of a

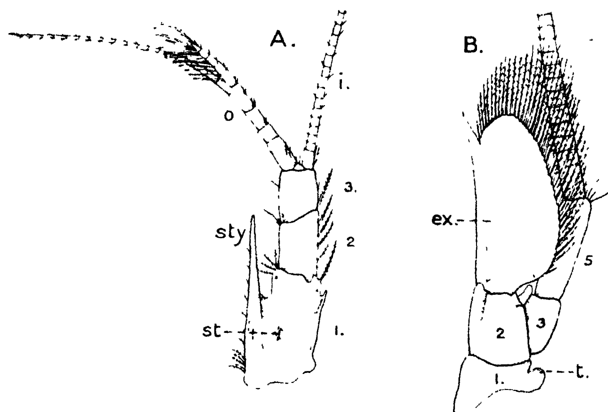


FIG. 156.

A, antennule, B, antenna, of *Athanas nitescens*. (After Sars.) 1-5, segments of the peduncle (the fourth segment in the peduncle of the antenna is not visible from above); *ex*, "scale" or exopodite of antenna; *i*, inner flagellum; *o*, outer flagellum of antennule with its inner branch bearing olfactory filaments; *st*, statocyst in basal segment of antennule; *sty*, stylocerite; *t*, tubercle bearing aperture of antennal gland.

half-tube ensheathing the outer flagellum and forming with its fellow of the other side a long siphon supposed to have a respiratory function. In *Albunea* (Hippidea), where by a rare exception only one flagellum is present, a respiratory siphon is formed by the apposition of the two antennules, which bear each a double longitudinal row of setae.

In the lower Decapoda the peduncle of the *antenna* has five segments, the two segments of the protopodite and the first three of the endopodite, but the segments are usually more or less displaced so as to articulate with each other in a zigzag manner (Fig. 156, B). The exopodite (*ex*) forms a large foliaceous "scale" (squama) in the Natantia. In most Reptantia the number of peduncular segments is reduced by the fusion of the second and

third, and the exopodite, when present, is often reduced to a spine-like "acicle." In the Scyllaridea the number of free segments is further reduced by the coalescence of the proximal segment with the epistome. In the Brachyura, the proximal segment is only distinct in the Dromiacea; in the other groups it is either fused with the epistome or, perhaps, represented by a small operculum (Fig. 147, B and C, *t*) which covers the external opening of the antennal gland. The exopodite is absent in all the Brachyura except possibly in certain Dromiacea (Homolodromiidae), where an immovable spiniform process is supposed to represent it. The flagellum is very short in most Brachyura and may disappear altogether. In some Corystidae the two flagella form a long respiratory siphon in much the same way as the antennules do in *Albunea*. In the Palinuridae not only the peduncle but also the flagellum is very stout, and in the Scyllaridae the whole appendage is expanded and flattened, and the flagellum is represented by a broad, shovel-like plate.

The *mandibles* never have a distinct lacinia mobilis, although, in some of the lower types (Atyidae), they may have a group of setae or spines on the inner edge. The incisor is widely separated from the molar process in many Caridea (Fig. 157, A), but in the other groups the two cannot be distinguished or are separated only by a groove. In some Caridea the incisor process is wanting. A palp of three segments is usually present, but the number of segments is sometimes reduced, and among the Caridea the palp is not unfrequently entirely absent either in isolated genera (*Hippolyte*, *Palaemonetes*) or throughout whole families (Crangonidae, Atyidae). In the Penaeidae the palp is expanded and lamellar, and apparently takes part in enclosing the respiratory passages.

The *maxillulae* (Fig. 157, B, and Fig. 9, B, p. 13) have two inwardly turned endites, and a palp which is sometimes divided into two, and even, in some species of *Penaeus* (Fig. 158, A), into three or four, segments. An outwardly turned plate (*ex*) directly connected with the proximal endite, and having the same relations as the large external plate of the maxillula of Euphausiacea, can sometimes be observed, but only exceptionally (*e.g.* *Caridina*) is it of considerable size. The chief difference from the maxillulae of the Euphausiacea consists in the absence of a distinct second segment, which here appears to be fused with the first.

The *maxillae* are closely comparable to those of Euphausiacea, though the relative proportions of the parts are very different. In the typical form such as we find in the Crayfish (Fig. 9, C, p. 13) the two endites are each divided into two by a deep incision, there is an unsegmented palp, and a very large lamellar expansion on the outer side to which the name *scaphognathite* is given. According to Hansen, the two bifid endites arise here, as in the Euphausiacea,

from the second and third segments of the limb. Coutière, however, states that in some primitive Caridea the double proximal

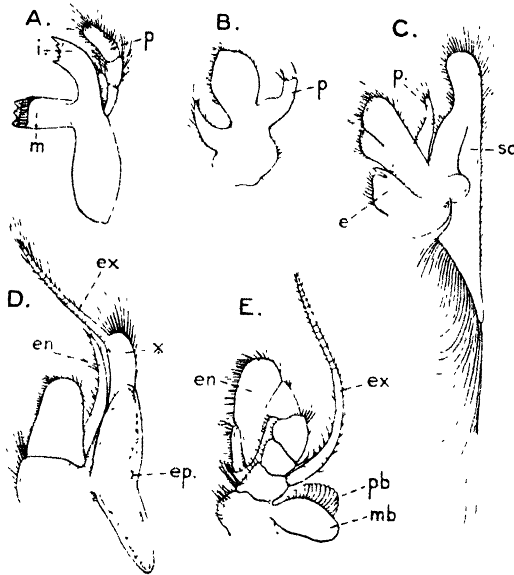


FIG. 157.

Mouth-parts of *Pandalus borealis* (Caridea). (After Sars.) A, mandible; B, maxillula; C, maxilla; D, first maxilliped; E, second maxilliped. *e*, proximal endite of maxilla (according to Boas, the small distal lobe alone represents the endite and the large proximal lobe does not represent the proximal division of the endite in other Decapoda); *en*, endopodite; *ep*, epipodite; *ex*, exopodite; *i*, incisor process; *m*, molar process of mandible; *mb*, mastigobranchia; *p*, palp; *pb*, podobranchia; *sc*, scaphognathite of maxilla: *, lobe on exopodite of first maxilliped characteristic of Caridea.

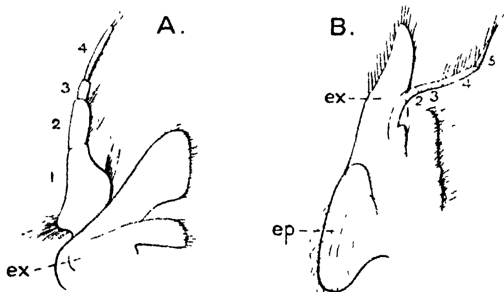


FIG. 158.

A, maxillula of *Penaeus caramote*; 1-4, palp of four segments; *ex*, exite connected with proximal endite. B, first maxilliped of same; 1-5, endopodite of five segments; *ep*, epipodite; *ex*, exopodite. (After Boas.)

endite can be seen to belong to the first segment, and that the other two lobes are independent of each other, belonging respectively

to the second and third segments. The scaphognathite has been variously interpreted as an epipodite or as consisting of epipodite and exopodite together. A comparison with the maxilla of the Euphausiacea shows, however, that it must be regarded as an extreme development of the plate which in the latter case is identified as the exopodite.

The modifications which this typical form undergoes within the Order are not very striking nor do they afford much material of systematic value. An undivided proximal endite is characteristic of the Caridea, in which group (with some few exceptions) it is also greatly reduced in size (Fig. 157, C). In the Pasiphaeidae both endites disappear.

It is characteristic of the Decapoda that the first three pairs of thoracic limbs are more or less distinctly differentiated from the others as *maxillipeds*. It must be noted, however, that the line of demarcation between the two groups of appendages is not always sharply drawn, and that in the Penaeidea and Caridea the third maxillipeds are often distinctly pediform.

In all Decapods, however, the *first maxilliped* (unlike the corresponding appendage of the Euphausiacea) has completely lost its pediform character. The endopodite is greatly reduced in size, and the coxopodite and basipodite are produced inwards as broad endites of which the proximal is often divided by an incision. The most primitive condition is found in certain Penaeidae (Fig. 158, B), where the endopodite presents the full number of five segments. In other Decapoda the number of segments is never more than two and the endopodite is often unsegmented. The exopodite is always present; in the Caridea (Fig. 157, D) it presents a characteristic lamellar expansion of its outer margin (lobe *a* of Boas), the narrow distal part corresponding apparently to the flagellum, which in the higher forms is segmented off from the peduncle and may be divided into numerous articulations. The epipodite is rarely absent (*e.g.* in many Anomura) and is especially large in the Brachyura (Fig. 159, A).

The *second maxilliped* departs less from the general type of the thoracic limbs than does the first. The proximal segments are not produced inwards as distinct endites. The endopodite is relatively short, permanently flexed inwards, and its distal part is commonly more or less flattened.

In the family Stylodactylidae (Caridea) the second maxillipeds appear to present an anomalous structure, two terminal segments articulating side by side on the end of the fifth segment. In the great majority of the Caridea (Fig. 157, E) the terminal segment articulates, not with the distal end but with the inwardly turned (morphologically the outer) margin of the preceding segment. The number of distinct joints is not infrequently reduced by the fusion

of the basipodite and ischiopodite. The exopodite is rarely absent (Sergestidae, Pasiphaeidae), and is often divided into a peduncle and a multiarticulate flagellum.

The *third maxilliped* may, in the Natantia, even exceed in length the next succeeding pair of appendages. The coxopodite and basipodite are almost always connected by an immovable articulation. In the Caridea the ischiopodite is quite coalesced with the meropodite, and the dactylopodite is obsolete or coalesced with the preceding segment. A serrate ridge or "*crista dentata*" (Fig. 147, A, mxp^3) is commonly present on the third segment, but no endites are developed from the first and second segments. Among the Brachyura (Fig. 147, B, C, mxp^3) the third maxillipeds become greatly modified to form an oper-

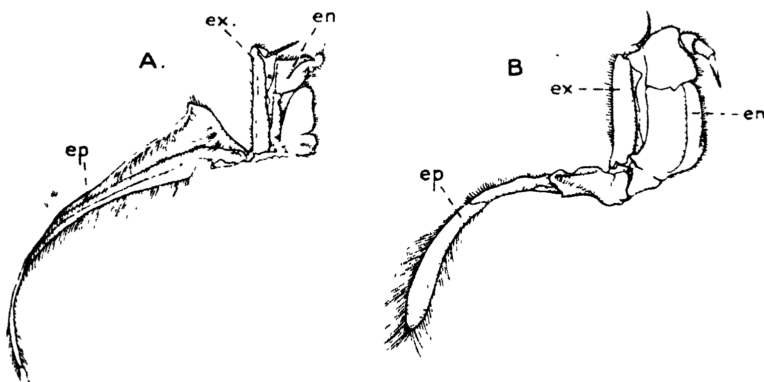


FIG. 159.

A, first, B, third maxilliped of *Neptunus pelagicus* (Brachyura). (After de Haan.) *en*, endopodite; *ep*, epipodite (mastigobranchia); *ex*, exopodite.

culum to the buccal frame and entirely lose their pediform character. The ischiopodite and meropodite become broad plates and the terminal three segments are often hidden behind the meropodite. The peduncle of the exopodite may also be expanded and share in forming the operculum. Its terminal flagellum is either folded out of sight or may be entirely lost. The epipodite forms a long curved blade in most Brachyura (Fig. 159, B, *ep*).

The remaining five pairs of thoracic appendages (*peraeopods*) are typically ambulatory legs, composed of the usual seven segments. Exopodites may be present on some or all of them in some Penaeidea and Caridea (Pasiphaeidae, Fig. 160, Hoplophoridae, some Atyidae, and Crangonidae), but elsewhere they are wanting. As a rule one or more pairs are chelate or sub-chelate, except in the Scyllaridea (where, however, the last pair are imperfectly chelate in the female sex) and in some Hippidea. The first three pairs are chelate in

most Penaeidea and in the Stenopidea and Astacura (Fig. 161), the first four or all five pairs in the Eryonidea (Fig. 162), the first two

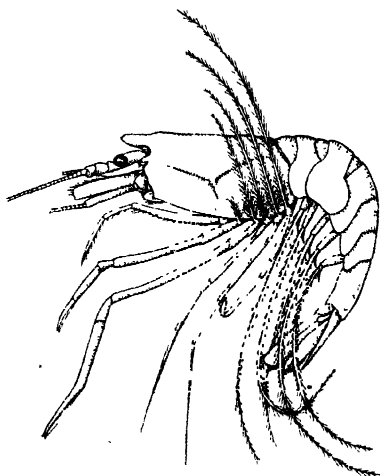


Fig. 160.

Psathyrocaris fragilis (Pasiphaeidae), showing the greatly developed exopodites of the thoracic legs (a 'Schizopod' character) and of the pleopods. (After Alcock.



Fig. 161.

Nephropsis Carpenteri (Nephropsidae), ♂. A deep-sea species in which the eyes have almost disappeared but the vestigial eye-stalk can be seen below the rostrum. (From Alcock, *Naturalist in Indian Seas.*)

in most Caridea, the first or the first two in Thalassinidea (Fig. 149, p. 260), and the first pair only in the other Anomura (Fig. 150,

p. 260) and the Brachyura. In most Anomura the last pair, and in a few Brachyura the last or the last two pairs, are subchelate. A very remarkable form of chela is found in the genus *Psalidopus* (Caridea) (Fig. 163), in which *both* fingers are movably articulated with the propodite, an arrangement resembling that found in the second maxilliped of *Stylodactylus*.

In most of the Reptantia, where the first pair of legs are chelate and much larger than the others, they are commonly referred to as the *chelipeds*, and the following four pairs are distinguished as walking-legs. Frequently the chelipeds are asymmetrical in size and shape on the two sides, the larger chela having the fingers armed with blunt crushing-tubercles, while the smaller has sharp cutting-teeth. In many cases, as, for instance, in the lobster, the larger crushing-chela may be on the right or the left side indifferently, but in some Brachyura it is constantly on the same side of the body. A curious reversal of asymmetry sometimes occurs as a result of the loss of the larger chela; at the next ecdysis the remaining chela assumes more or less completely the characters of a large crushing-chela, while the regenerating limb has the form of a small cutting-chela.

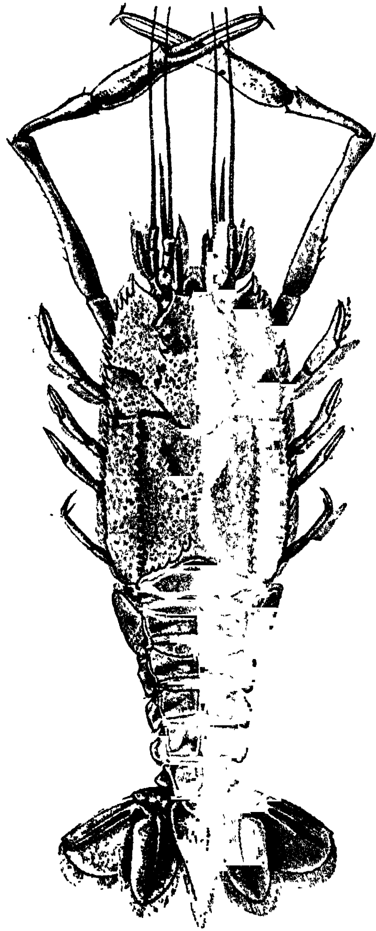


FIG. 162.

Pentacheles beaui (Eryonidea). The vestigial eye-stalks are fixed in notches in the front of the carapace. (From Alcock, *Naturalist in Indian Seas*.)

A modification of some of the legs as swimming-paddles occurs in various groups, for instance, in the Portunidae (Brachyura), where the last pair are so modified. In some Natantia and in one genus of Hippidea one pair of legs may become multiarticulate and flagelliform. This modification occurs especially in the second pair of many Caridea (formerly grouped together as Polycarpinea) (Fig. 148), where the

carpopodite and sometimes also the meropodite and ischiopodite are subdivided into small articulations.

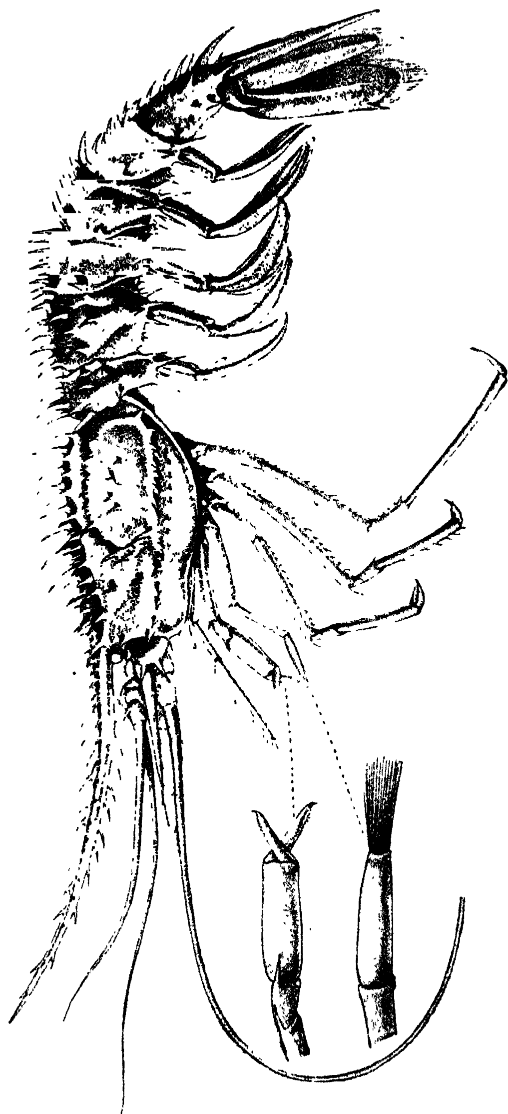


Fig. 163.

Psalidopus spiniventris (Caridea). As shown in the enlarged figures at the side, the first legs have peculiar chelae in which both fingers are movable, while the second legs terminate in a brush of setae. (From Alcock, *Naturalist in Indian Seas*.)

While in the Natantia, with few exceptions, all the seven segments of the limb are distinct and movable, among the Reptantia

this is only the case in the Eryonidea. In the Astacura the first pair, and in the remaining Reptantia all the five pairs, of legs have the basipodite and ischiopodite immovably united. Perhaps correlated with this fusion is the presence of a "fracture plane" in the basipodite, at which separation of the limb takes place in autotomy in many Reptantia.

In a few Decapoda some of the legs become quite vestigial or even disappear altogether. In the Sergestidae the last two pairs are reduced, and in *Acetes* the last pair and in *Leucifer* the last two are quite absent. In the Pinnotheridae (Brachyura) the last pair may be rudimentary or absent. In many Crangonidae the second pair are smaller than the others, and in *Paracrangon* they disappear entirely. This case is especially noteworthy since the suppression of members of a meristic series rarely occurs except at one end of the series.

The epipodites and associated structures of the thoracic limbs will be described below in connection with the branchial system.

The *pleopods* of the Decapoda present typically the same structure as those of the Euphausiacea. Of the two segments composing the protopodite the first is usually small, often apparently absent, the second elongated and often stout. The two rami may be multi-articulate and flagelliform, more often flattened and unsegmented, and bear a marginal fringe of natatory setae. The endopodite may bear on its inner margin an *appendix interna* tipped with a group of coupling-hooks.

It is interesting to note that the Penaeidea and Stenopidea, which, on the whole, take the lowest place among the Decapods, never possess an appendix interna (except in so far as an element derived from it may possibly share in forming the copulatory appendage on the first pair of pleopods in the male), though the presence of that organ in the Leptostraca, Euphausiacea, and Stomatopoda shows that its possession must be reckoned a primitive feature among the Malacostraca.

The pleopods are most strongly developed in the Natantia, where they form the chief swimming-organs. In the Reptantia the natatory function is less important and the pleopods are generally feebler, though in some fossorial Thalassinidea they are of considerable size. An appendix interna is wanting except in some Thalassinidea and in the Scyllaridea, where the pleopods are peculiarly modified. In the Anomura, excluding the Thalassinidea, the pleopods are generally feeble, often uniramous, and are sometimes absent from the first somite, as they are also in the Scyllaridea and Parastacidae. They are absent altogether in the males of Hippidea, Lithodidae, and of some other Paguridea; when present in the Paguridea, they are, as a rule, developed only on one side of the body and an appendix interna is sometimes present. In the Brachyura the first and second pairs (which are specially

modified, as described below) alone persist in the male, while in the female the second to the fifth pairs are (with rare exceptions) developed as egg-carrying appendages, with short protopodite and long and slender rami; the first pair are absent in the female except in the Dromiacea. In *Callianidea* (Thalassinidea) the rami of the pleopods are fringed with long filaments, apparently branchial in function; this isolated case forms a curious parallel to the development of branchial filaments on the pleopods in the Stomatopoda and in *Bathynomus* among the Isopoda.

Sexual modifications are commonly presented by the pleopods, most constantly by those of the first and second pairs, which in the male assume a copulatory function. In the case of the first pair the difference may be slight, as in most Caridea, where the endopodite is reduced to a small leaflet, differing more or less in shape in the two sexes, and in the male armed with a group of coupling-hooks. In the Penaeidea the first pair of the female have the endopodite small or wanting; in those of the male it is represented by a membranous plate, often of large size and complicated structure, attached to the inner side of the peduncle, and bearing (as in the Caridea) a group of coupling-hooks which interlock with those of the other side. To this apparatus the name of *petasma* has been given by Spence Bate. In the Reptantia the appendages of this pair are never biramous. In the female sex they are greatly reduced in size or altogether absent. Occasionally they are absent in both sexes (Parastacidae, Scyllaridea, some Paguridea, and Hippidea), but more commonly they are developed in the male into copulatory appendages, usually styliform, with a spoon-shaped or tubular terminal part. In some Thalassinidea (*Upogebia*), by a rare exception, these appendages are present (uniramous) in the female but absent in the male sex.

The second pair in the female sex are almost always similar to those which follow. In the male sex, however, this is rarely the case (some Scyllaridea, Parastacidae, *Upogebia*). As a rule, they are modified by the development of an accessory process, the *appendix masculina* (Boas), from the inner edge of the endopodite. This appendix is small in the Penaeidea and Caridea (in which latter it may coexist with the appendix interna), but in the other groups it increases in importance, the terminal part of the endopodite diminishing, as does also the exopodite, until in the Brachyura (and some Anomura) there remains only a styliform appendage of two segments, the proximal representing the protopodite and the distal the endopodite together with its appendix masculina.

The *uropods* retain in the Macrurous groups the general characters of the caridoid type, having a short protopodite and broad lamellar rami, forming with the telson a tail-fan. As a rule the exopodite is more or less distinctly divided by a transverse

joint, and very rarely as in *Laomedia* (Thalassinidea) the endopodite is similarly divided.

Among the Anomura the uropods are variously modified. In the Galatheidea they retain more or less the type of structure which they showed among the Macrura. In most Paguridea they become modified as organs for fixing the posterior end of the body in the shell or other lodging carried by the animal, the rami are stout and curved, with roughened, "file-like" surfaces which are pressed against the shell, and the appendages of the two sides share in the asymmetry of the whole abdomen. In the Lithodidae alone among Anomura the uropods are wanting. This is all but universally the case also among the Brachyura, where only in certain Dromiacea (Dromiidea) are there found traces of uropods in the form of small plates intercalated on each side between the last abdominal somite and the telson.

Branchial System.—With the single exception of the aberrant genus *Leucifer*, all Decapoda possess branchiae connected with some or all of the thoracic somites and lying in the cavities enclosed by the branchiostegites on each side. The typical number of branchiae which may be present on each side of a somite is four, arranged as follows: One is attached to the lateral wall of the somite dorsal to the articulation of the appendage (*pleurobranchia*), two to the articular membrane between the coxopodite of the appendage and the body-wall (*arthrobranchiae*), and one, representing a differentiation of part of the epipodite, is inserted on the coxopodite itself (*podobranchia*).

Four series of gills corresponding to these can be traced in a more or less incomplete form throughout the whole series of the Decapods. They are, however, not invariably distinguished from each other by the position of attachment in the manner just described. In particular, the distinction between arthrobranchiae and pleurobranchiae is often very difficult to draw in practice, and there are some cases where an arthrobranchia in one species is plainly homologous with a pleurobranchia in another. Claus has shown that in the development of *Penaeus* three bud-like outgrowths appear on the proximal part of most of the thoracic limbs (Fig. 164, A). The distal one (*a*) gives rise to the epipodite with its podobranchia and the two others (*b*, *c*) are the arthrobranchiae. As development proceeds an apparent change in the position of these last is brought about by coalescence of the proximal part of the appendage with the body, so that the branchiae no longer appear as outgrowths of the limb but spring from that part of the body-wall which afterwards forms the articular membrane of the joint. The pleurobranchia appears a little later than the other two (Fig. 164, B, *d*), but its place of origin is very close to if not actually on the basal part of the limb itself. Williamson has observed a

similar transference of the gills from the limb to the body-wall in the development of *Crangon* (Caridea), and Bouvier in *Uroptychus* (Galatheidea). Claus concludes from these observations that not only the podobranchiae but also the arthro- and pleurobranchiae are originally appendages of the limb. The absorption of the proximal part of the limb into the body-wall is of importance in view of Hansen's recognition of a pre-coxal element in the appendages of various Crustacea.

The origin of the podobranchiae by differentiation of part of the epipodite is also clearly shown in the development of *Penaeus*. The most distal of the three outgrowths mentioned above early becomes bilobed. The distal lobe, which lies in front of the

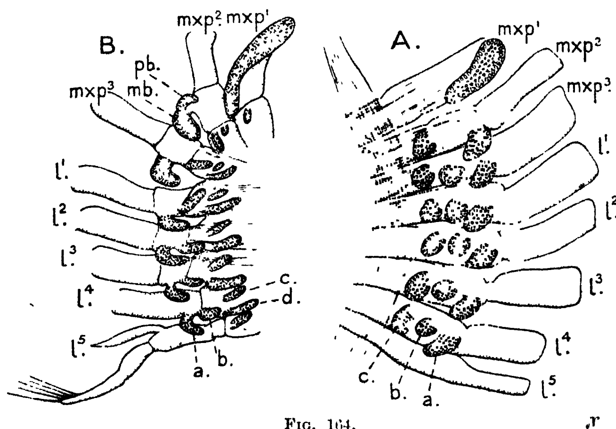


Fig. 164.

Two stages in the development of the branchial system of *Penaeus*. (After Claus.) A, early stage; B, later stage after appearance of the rudiments of pleurobranchiae. mxp^1-mxp^3, maxillipeds; l^1-l^5, legs; *a*, distal series of rudiments giving rise to mastigobranchiae and podobranchia (on mxp^2); *b*, *c*, rudiments of arthrobranchiae; *d*, rudiments of pleurobranchiae. In B the distal rudiment on mxp^2 is dividing into podobranchia (*pb*) and mastigobranchia (*mb*).

proximal one, develops in the case of the second maxilliped (Fig. 164, B, mxp^2) into the podobranch (in the other appendages it disappears), while the proximal and posterior lobe becomes the epipodite or *mastigobranchia* of the adult, a bilobed membranous lamina which extends upwards into the branchial chamber between the gills. On the first pair of maxillipeds the distal lobe remains simple and persists as the distal part of the laminar epipodite of the adult. It is remarkable, however, that in the only cases in which the epipodite of the first maxilliped develops branchial filaments (in some Parastacidae), these are borne, not by the distal part which appears to represent the podobranchia, but by the proximal division.

In most Reptantia the podobranchiae have a similar relation to the mastigobranchiae to that just described in *Penaeus*. In the

Astacidae, however, the axis of the gill coalesces with the mastigobranchia, which has the form of a folded membranous lamina from which the branchial filaments spring directly. In the Parastacidae this lamina is greatly reduced or disappears.

In the Caridea, the mastigobranchiae, when present, have usually the form of short curved rods, directed backwards, each ending in a hooked process which grasps a tuft of long slender setae on the coxopodite of the next succeeding appendage. This tuft of setae, which is also present in some Reptantia, springs from a small papilla which Coutière has compared with the setiferous epipodial process found in *Gnathophausia* (Mysidacea) (Fig. 106, *ep*, p. 176), and which he regards as a distinct element of the branchial system (*setobranchia* of Borradaile). In a species of *Eiconaxius* (Thalassinidea) Coutière has found that the coxopodite of the first leg bears *two* podobranchiae, one attached as usual to the base of the mastigobranchia, the other close to, if not actually inserted on, the setobranchia. In no other Decapod is more than one podobranchia found on any limb.

As regards their structure, each branchia consists of a stem or axis which is attached at or near one end and bears numerous lateral branches. According to the form and arrangement of these latter, three main types of gills have been distinguished, which, however, are connected by intermediate forms. In the *trichobranchiate* type (Fig. 165, B) the branches are filamentous, and are arranged in several series around the axis. In the *phyllobranchiate* type (Fig. 165, C) the branches are flattened laminae, and as a rule only two opposite series are present. The *dendrobranchiate* type (Fig. 165, A) is characterised by the fact that the biserial primary branches are themselves ramified, sometimes in a very complex fashion. The dendrobranchiate type is peculiar to the Penaeidea, but each of the other two types recurs in widely separated groups. Thus the Caridea have phyllobranchiae, as have also all the Brachyura, with the exception of some of the primitive Dromiacea, which have trichobranchiae. The Stenopidea, Palinura, and Astacura have trichobranchiae. Among the Anomura, phyllobranchiae are the rule, but *Aeglea* among the Galatheidea, and the Pylochelidae, with several genera of Paguridae among the Paguridea, have trichobranchiae, and the gills of some Thalassinidea are intermediate in character.

In the number and arrangement of the gills very great differences exist, which afford valuable systematic characters. At the same time, the important divergences sometimes presented by closely allied forms render it necessary to use caution in estimating the value of these characters (compare, *e.g.*, *Caridina* and *Limnocaridina*, or *Pandalus* and *Pandalina*). The last thoracic somite is invariably destitute of mastigobranchia, podobranchia, or arthro-

branchiae, though it may carry a pleurobranchia and a setobranchia. As a rule no gills are present on the first thoracic somite, but in some Penaeidea, Stenopidea, Astacura, and Thalassinidea, a minute arthrobranchia (? pleurobranchia) is present, while in some Parastacidae the epipodite bears some branchial filaments and is, in fact, a rudimentary podobranchia.

On the remaining somites the podobranchiae are the most frequently suppressed. It is characteristic of the Scyllaridea and Astacura that they possess a full series of podobranchiae, and less complete series are found in the more primitive Penaeidea (Cerataspinae and Aristeinae), in the Eryonidea and some Thalassinidea, and in the primitive Homolodromiidae among the Dromiacea. In

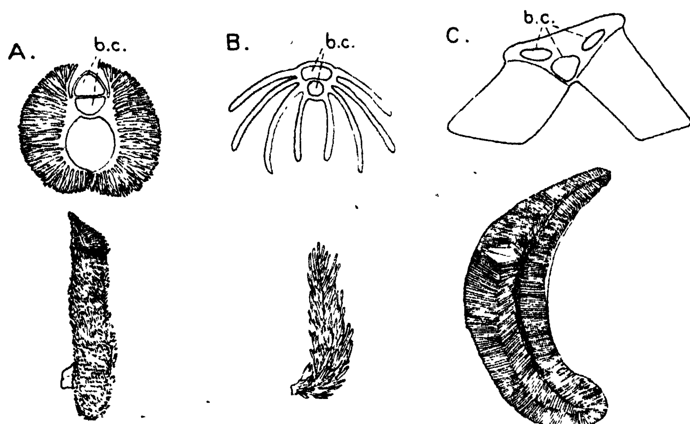


Fig. 165.

Branchiae of Decapoda. The lower figures show the complete branchiae, the upper figures transverse sections of the same. A, dendrobranchiate type (*Penaeus canaliculatus*). B, trichobranchiate type (*Astacus fluviatilis*). C, phyllobranchiate type (*Palaemon lar*). *b.c*, blood-channels in axis of branchia.

all other Decapods they are absent from the legs and, except in Brachyura, from the third, though not uncommonly present on the second, maxillipeds. Apart from the podobranchiae, the mastigobranchiae and setobranchiae may persist in a more or less complete series, especially in the Caridea. The pleurobranchiae are stated to extend forwards to the somite of the third maxilliped in some Caridea, and to that of the second in the Penaeidae; but it must be noted that the distinction between pleuro- and arthrobranchiae in the crowded anterior part of the branchial chamber is often obscure. They form the chief part of the gill-system in the Caridea, where five are usually present, and, on the other hand, they are quite wanting in most of the Thalassinidea. In the Brachyura a formula of nine branchiae on each side is found in all the main subdivisions; but while it is practically universal in the Oxyrhyncha

and in those families of the Brachyrhyncha formerly grouped together as Cyclometopa, it suffers reduction in many of the Catometopa, especially in terrestrial and parasitic forms, and in the majority of the Oxystomata.

The table on p. 280 gives the branchial formulae in a series of representative forms.

The arrangements for maintaining a current of water through the branchial chamber and for preventing the ingress of foreign particles are very varied and often complex. The branchial current is caused by the vibratory movements of the scaphognathite or exopodite of the maxilla, and as a rule it sets from behind forwards, though it appears that in some cases, especially in Decapods which burrow in sand or mud, the direction of the current is periodically reversed. In the simplest cases, as in most of the Macrurous groups, the water enters along the lower margin of the branchial chamber, which is protected by setae, and in particular by those of the setobranchiae. The exhalent current passes out at the sides of the oral region in front. This arrangement is modified in the Brachyura by the free edge of the branchiostegite fitting closely to the bases of the legs on each side, only leaving an aperture for the ingress of water in front of the base of the cheliped. This aperture is provided with an opercular valve formed by the base of the long epipodite of the third maxilliped. These arrangements may be further complicated in various ways, especially in the case of burrowing forms. The exhalent passages, which in some cases may by reversal of the current become inhalent, are not unfrequently prolonged towards the front of the head by the apposition of various appendages. In many Penaeidea the lamellar mandibular palps, the antennal scales, and the antennular peduncles co-operate to this end; in the Brachyura and some Anomura the flattened third maxillipeds carry the exhalent channels at least as far as the anterior margin of the buccal frame; the flagella of the antennules in some Hippidea and of the antennae in the Corystidae form a long exhalent (or inhalent) siphon; and in the Leucosiidae among the Brachyura the inhalent as well as the exhalent channels are carried forwards to the front of the head beneath the expanded maxillipeds. Some special adaptations for aerial respiration will be described below in connection with the circulatory system.

Alimentary System.—The stomodaeal "stomach" of the Decapods is developed into a triturating and straining apparatus of great complexity. The simplest form of the gastric armature appears to be found in the Penaeid genus *Cerataspis* (Fig. 166), recently studied by Bonnier. Here the chitinous lining of the stomach, although provided with numerous internally projecting ridges armed with setae and spinules, is nowhere indurated or calcified to form distinct sclerites such as are found in other Decapods, and in so far it

TABLE OF BRANCHIAL FORMULAE.

NOTE. The numbers indicate well-developed branchiae. m. = mastigobranchia; r. = vestigial branchia.

		Maxillipeds. I.			Maxillipeds. II.			Maxillipeds. III.			Legs. IV.			Legs. V.			Legs. VI.			Legs. VII.			Legs. VIII.			Total.
		Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	
Penaeidea	*Penaeus (caramote)*	m.	1	0	1 m.	1	1	m.	2	1	m.	2	1	m.	2	1	m.	2	1	0	1	1	0	0	1	19+6 m.
	Benthesicymus	m.	1	0	1 m.	1	1	1 m.	2	1	1 m.	2	1	1 m.	2	1	1 m.	2	1	m.	2	1	0	0	1	24+7 m.
	Sergestes	m.	0	0	1 m.	0	r.	0	0	1 r.	0	0	1 r.	0	0	1 r.	0	0	2	0	0	2	0	0	0	8+4r.+2m.
Stenopidea	*Stenopus*	m.	1	0	1 m.	1	0	m.	2	1	m.	2	1	m.	2	1	m.	2	1	m.	2	1	0	0	1	19+7 m.
Caridea	*Pandalus*	m.	0	0	1 m.	0	0	m.	2	0	m.	1	1	m.	1	1	m.	1	1	m.	1	1	0	0	1	12+7 m.
	Palaemon	m.	0	0	1 m.	0	0	m.	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	8+3 m.
	Spirontocaris (spinus)	m.	0	0	1 m.	0	0	m.	0	0	m.	0	1	m.	0	1	m.	0	1	0	0	1	0	0	1	6+6 m.
	Hippolyte (viridis)	m.	0	0	m.	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	5+2 m.
	Crangon (vulgaris)	m.	0	0	m.	0	0	m.	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	6+3 m.
	Hoplophorus	m.	0	0	1 m.	0	0	m.	2	0	m.	1	1	m.	1	1	m.	1	1	m.	1	1	0	0	1	12+7 m.
	Atya	m.	0	0	1	0	0	m.	2	0	m.	1	1	m.	0	1	m.	0	1	m.	0	1	0	0	1	9+6 m.
	Limnocaridina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	4
	Pasiphaea (sivado)	m.	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	8+m.
Astacura .	*Homarus*	m.	0	0	1 m.	0	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	1 m.	2	1	0	0	1	20+7 m.
Palinura .	*Palinurus*	m.	0	0	1 m.	1	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	1 m.	2	1	0	0	1	21+7 m.
Anomura	*Thalassina*	0	0	0	1 m.	1	0	1 m.	2	0	1 m.	2	0	1 m.	2	0	m.	2	0	m.	2	0	0	0	0	15+6 m.
	Axius	m.	0	0	1 m.	r.	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	m.	2	1	0	0	r.	18+2r.+7m.
	Upogebia	0	0	0	0	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	0	10
	Galathea (squamifera)	m.	0	0	0	0	0	m.	2	0	m.	2	0	m.	2	1	m.	2	1	0	2	1	0	0	1	14+5 m.
	Coenobita	0	0	0	0	0	0	0	r. r.	0	0	r. r.	0	0	2	1	0	2	1	0	2	1	0	0	1	10+4 r.
	Eupagurus and *Lithodes*	0	0	0	0	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	1	0	0	0	11
Brachyura	*Homolodromia*	m.	0	0	1 m.	1	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	0	2	1	0	0	1	20+6 m.
	Dromia	m.	0	0	1 m.	0	0	m.	2	0	m.	2	0	0	2	1	0	2	1	0	1	1	0	0	1	14+4 m.
	Cancer	m.	0	0	1 m.	1	0	1 m.	2	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	9+3 m.
	Ocypoda	m.	0	0	1 m.	0	0	1 m.	2	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	7+3 m.
	Ilia	m.	0	0	m. r.	0	0	m. r.	2	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	6+3 m.
	Pinnotheres	m.	0	0	0	0	0	m.	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3+2 m.

resembles that of many of the more primitive Malacostraca. A deep transverse infolding of the dorsal surface, which marks the division into the larger anterior or cardiac and the smaller posterior pyloric chamber, is produced internally into a strong median tooth (*m.t*). The floor of the cardiac chamber presents internally a median (*m.r*) and a pair of lateral (*l.r*) longitudinal ridges defined by deep foldings of the cuticle and representing elements which in other forms become calcified sclerites; just above these on each side are series of stout denticles (*d*), of which a posterior group in the vicinity of the "median tooth" appear to correspond to the "lateral teeth" of other Decapods. The pyloric division has its lumen greatly reduced by infoldings of its walls, and may be regarded as being divided by a longitudinal fold (*r*) on each side into a dorsal and a ventral portion,

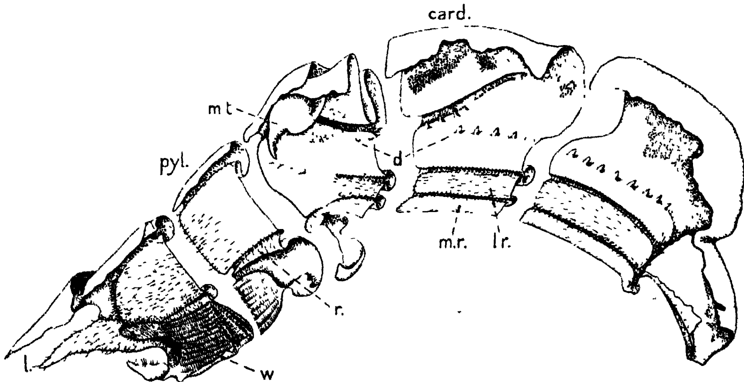


Fig. 166.

Dissection of the stomach of *Ceratospis monstruosus* (semi-diagrammatic). *card*, cardiac chamber; *d*, lateral denticles; *l*, terminal lappets projecting into mid-gut; *l.r*, lateral ridge; *m.r*, median ventral ridge of cardiac chamber; *m.t*, median tooth; *pyl*, pyloric chamber; *r*, longitudinal ridge separating dorsal and ventral divisions of pyloric chamber; *w*, wedge-shaped ridge with straining apparatus. (After Bonnier.)

of which the former is a direct continuation of the cardiac chamber, while the latter is a diverticulum closed in front and communicating with the dorsal chamber only by a narrow slit between the setose margins of the longitudinal ridges. The ventral chamber has its cavity again divided into two portions by a strong median wedge-shaped ridge (*w*) which rises from its floor and is produced posteriorly into a tongue-like process overhanging the apertures of the hepatic ducts into the mid-gut. The lateral surfaces of this ridge are provided with a characteristic armature which seems to act as a straining apparatus; it consists of numerous parallel plate-like ridges running longitudinally and standing at right angles to the surface, each bearing on its edge a comb-like fringe of setae lying parallel with the surface and covering in the groove lying between each ridge and the next. This wedge-shaped ridge and

straining apparatus appear to be very constant throughout the group, and are no doubt homologous with the very similar structures found in other orders of Malacostraca. At its posterior end the chitinous lining of the stomodaeum terminates in four tongue-like lappets (l) (much elongated in *Penaeus*) which project freely into the cavity of the mid-gut.

In the other Penaeidea the stomodaeal armature is much more complex than that just described. A large number of sclerites, more or less calcified, are differentiated in the walls of both cardiac and pyloric chambers. A dorsal and a ventral series can be distinguished, the dorsal and dorso-lateral pieces of the cardiac chamber being in relation to the strong median and lateral teeth. From this arrangement of the parts found in the Penaeidea, that characteristic of the Reptantia may be easily derived, the chief differences being due to the appearance of additional sclerites, and especially of a series of intermediate pieces on the lateral walls of the two chambers. The elements of the dorsal series are the more important, forming as they do a system of levers moving the dorsal and lateral teeth.

The great majority of the Caridea diverge more widely from the Penaeid type owing to the disappearance of the whole of the dorsal series of sclerites and of the dorsal and lateral teeth associated with them, the roof of at least the cardiac chamber remaining quite membranous. Only the Atyidae and one or two others among the families of Caridea hitherto examined possess certain elements of the dorsal series well developed, but they are differently arranged from those of the other Decapods.

Mention must be made here of the gastroliths or "crab's eyes," which are discoidal calcareous nodules in the lateral walls of the cardiac division of the stomach in Crayfish (*Astacus*) and Lobsters (*Homarus*). They are periodically formed shortly before ecdysis takes place, and are shed into the cavity of the stomach, to be broken up and dissolved, apparently providing some of the material necessary for the calcification of the new integument. No similar structures are definitely known to occur in any other group of Decapods.

The mid-gut varies very much in length in different Decapoda, but exact observations have been made only on a few types. In the Crayfish (*Astacus*) it is exceedingly short, so that the dorsal lappet which terminates the cuticular lining of the stomodaeum extends through it into the beginning of the proctodaeum. In most, if not all, Brachyura it is also very short. In the Lobster (*Homarus*), however, it occupies five-sixths of the post-gastric part of the alimentary canal. In species of *Alpheus* (Caridea) the mid-gut extends as far as the last somite, and in *Paguristes* it is longer than the proctodaeum. From the upper surface of the mid-gut

there arises anteriorly in Astacura and most Thalassinidea a short unpaired caecum. In *Callianassa* among the Thalassinidea and in most Paguridea a pair of longer or shorter caeca are present, and in most Brachyura they form two long and convoluted tubules. In the Caridea and Galathaeidea and in *Pagurristes* (Paguridea) no caeca are found. *Dromia* possesses a single short caecum, and so resembles the Astacura and differs from the other Brachyura.

An unpaired caecal tube of considerable length springs from the dorsal surface of the intestine in the Brachyura, and a shorter caecum is present in the Lobster, in the Thalassinidea, and in some Paguridae. It is probable that in all these cases the caecum arises from the posterior end of the mid-gut. In *Alpheus*, according to Coutière, the mid-gut is produced backwards beyond its junction with the narrower hind-gut into a number of blind saccules.

Groups of gland-cells on the walls of the oesophagus, on upper and lower lips, and on the maxillulae and maxillae, have been regarded as salivary glands. Quite similar glands, however, may occur throughout the whole length of the hind-gut also, and they are identical in structure with the dermal glands which occur in various situations on the surface of the body.

With the single exception of *Leucifer*, which possesses only two pairs of hepatic caeca, the voluminous "liver" of the Decapods consists of a mass of minutely ramified tubules, lying mainly in the thorax. It communicates with the anterior part of the mid-gut by, as a rule, a single duct on each side, but in *Alpheus* (Coutière) three ducts are present. In Paguridae the hepatic glands are displaced backwards, and lie for the most part in the abdominal region.

Circulatory System.—The heart in all Decapods is short, polygonal in outline, and situated under the posterior part of the carapace. As a rule there are three pairs of venous ostia, of which one, or in the Brachyura two pairs are situated on the upper surface. Coutière has demonstrated the existence of two additional pairs in certain Caridea, and possibly further research will show that these are present in other cases.

Anteriorly the heart gives off a median ophthalmic artery which runs forward to supply the region of the eyes. On each side of this originates an antennal artery, which, besides supplying the antennae, sends branches also to the rostrum, eyes, and adjacent parts. In *Astacus*, Bouvier finds that terminal branches of the antennal arteries unite in front of the brain in a median vessel which runs backwards to anastomose on the walls of the oesophagus with branches of the sternal (subneural) artery—an arrangement which recalls the circumoesophageal vascular ring of some Isopoda and Amphipoda. A second pair—the hepatic arteries—arise from the sides of the heart a little way behind the antennal arteries, and are distributed to the hepatic glands and adjacent viscera.

Posteriorly the heart sends off a median vessel, the superior abdominal artery, while the unpaired descending artery (sometimes called the sternal artery) may arise separately from the heart (Brachyura) or may branch off from the superior abdominal artery just beyond the valves which mark its origin from the heart.

The descending artery passes on one side (either to right or left) of the intestine and pierces the ventral nerve-chain in nearly all Decapods, passing between the connectives uniting the sixth and seventh thoracic ganglia. Only in some of the Brachyura, where the concentration of the nervous system reaches its highest point (Oxyrhyncha and some Brachyrhyncha), this perforation of the nerve-mass does not take place, the artery passing behind instead of through it. On arriving at the ventral surface the artery bifurcates in the median plane, a large branch, to which the name of sternal artery is commonly applied, running forwards to supply the ventral surface of the thorax and its appendages, while a smaller branch running backwards also beneath the nerve-chain is the inferior abdominal artery (absent only in Paguridea). These two arteries taken together form a median longitudinal trunk quite comparable to the subneural vessel of Isopods, and, like it, may communicate with the dorsal system of vessels by a circumoesophageal ring. A further communication is very often present at the posterior end of the abdomen, where a vascular ring encircling the intestine unites the superior and inferior abdominal arteries. A pair of posterior lateral arteries arising from the superior abdominal artery near its origin from the heart, and often unsymmetrically developed, are of importance since they irrigate the branchiostegal regions of the carapace which have a respiratory function.

A venous sinus in the mid-ventral line receives the blood from the lacunar system of the body and appendages and distributes it to the gills, whence it is returned to the pericardial sinus by branchio-pericardial channels running in the inner wall of the branchial cavity. A minor circuit for the blood is afforded by the lacunar network of the branchiostegites, which, receiving blood partly from arteries and partly from adjacent venous sinuses, return it directly to the pericardium by special channels.

In terrestrial Decapods various modifications of the respiratory and circulatory systems are met with. In those most completely adapted to a terrestrial life (*Birgus*, *Cardisoma*) the lining membrane of the branchial cavity is very vascular and covered with minute villi. The supply of venous blood to the sinuses of the branchiostegal regions is more important and more definite than in aquatic Decapods, and the apparatus no doubt functions as a lung. In the terrestrial Hermit-crabs (*Coenobita*) a very peculiar respiratory organ is found. A rich vascular network is developed

in the delicate skin of the abdomen, especially on the dorsal side anteriorly. Two pairs of venous trunks running along the sides of the abdomen return the blood to the pericardium, a pair of rhythmically contractile vesicles at the base of the abdomen serving to accelerate the flow.

Excretory System.—In all Decapods the antennal gland is well developed, and generally presents a complexity of structure not found elsewhere among Crustacea. It has in most cases lost its original tubular form and assumed that of a compact gland. Three divisions are commonly distinct—the saccule, the labyrinth, and the bladder, with its efferent duct leading to the exterior. The saccule, which represents the end-sac of the typical antennal gland, may retain its simple saccular form, but more commonly it is complicated either by the development of partitions dividing up its cavity, or by numerous branches which ramify through the mass of the labyrinth. The labyrinth may be considered as derived from a sac which, by the rich development of partitions and trabeculae from its walls, has been converted into a spongy mass traversed by a complex system of canals. In the Crayfish (*Astacus*) the structure is still further complicated, mainly by the elongation of a portion of the labyrinth into a whitish cord of spongy substance which is convoluted upon itself, forming the "medullary" portion of the gland, the greenish "cortical" layer representing the proximal portion of the labyrinth which communicates with the end-sac. The bladder may retain, as in the Crayfish, the form of a simple vesicle communicating with the exterior by a short duct. In many cases, however, it sends off prolongations which may extend through a great part of the body. In some Caridea this vesical system is very extensive, lobes from the two sides uniting with each other to form an unpaired vesicle above the stomach. In the Brachyura three main lobes are given off from the bladder, which are very constant throughout the group, such differences as do occur being correlated with the differences in shape of the carapace. In the Paguridae, however, the vesical system reaches its greatest complexity (Fig. 167). The bladder sends off prolongations which ramify between the organs and anastomose to form delicate networks and arborisations in the region of the thorax, and two long diverticula, which may unite with each other, pass backwards to traverse the whole length of the abdomen. In *Palinurus* an accessory gland not found in any other type opens into the duct of the bladder. The external aperture is in most cases placed on a papilliform elevation on the proximal segment of the antennal peduncle. In the Brachyura the aperture is covered by an operculum (Fig. 147, B and C, *t*), capable of being opened and closed by special muscles. It has been shown that this operculum in all probability represents the

reduced proximal segment of the antenna, and the muscles attached to it have been identified with those which move the proximal antennal segment in the lower Decapods. This structure was described by Audouin and Milne-Edwards as a kind of auditory ossicle.

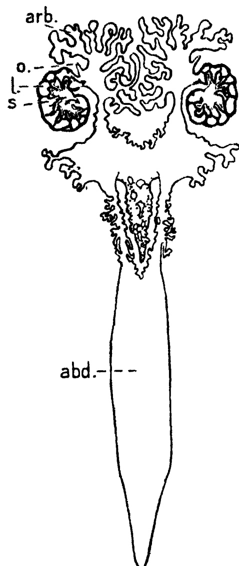


Fig. 167.

Diagram of the excretory system of *Eupagurus bernhardus*. *abd*, unpaired vesicle lying in abdomen; *arb*, arborisations of the vesical system in thorax; *l*, labyrinth; *o*, external opening; *s*, saccule. (After Marchal.)

No trace of the maxillary gland is known to persist in any adult Decapod, though it is frequently well developed in the larval stages.

Traces of glandular organs, presumed to be homologous with the antennal and maxillary glands, have been observed in embryonic stages in certain other somites of the trunk. In addition, certain other structures are found in adult Decapods, the excretory functions of which have been demonstrated physiologically, although their morphological significance remains obscure. The most important of these are the "branchial glands," which are masses of connective-tissue cells surrounding the venous channels in the axis of the gills and are devoid of ducts. Other glands of the dermal type also occur in connection with the gills.

Nervous System.—Great differences exist in the number and disposition of the ganglia composing the ventral chain. Among the lower Decapods the six ganglia corresponding to the six abdominal somites are distinct, but those of the cephalothorax may be more or less coalesced. The largest number of distinct ganglia appears to be found in the Astacura, where those of the five posterior thoracic somites are well separated, the remaining cephalothoracic ganglia being more or less completely coalesced to form a large suboesophageal ganglion. In other cases coalescence has taken place to a greater extent, and in the Scyllaridea and some Caridea, at least, all the cephalothoracic sternal ganglia form a single mass. Among the Anomura the degree of coalescence varies, and sometimes the first abdominal ganglion is approximated to the thoracic mass. Among the Brachyura the concentration of the nervous system reaches its highest point; the whole of the sternal ganglia are united into a rounded mass lodged in the thorax, from which the nerves radiate outwards. As a rule this mass is perforated in the centre for the passage of the descending artery. In the more primitive Dromiacea, however, the concentra-

tion is somewhat less complete, the outlines of five pairs of ganglia can be distinguished in the central mass, while posteriorly is a shortened chain of five pairs of ganglia corresponding to the abdominal somites, although not extending beyond the posterior limits of the thorax.

A system of visceral nerves is well developed in the Decapoda. A gastric plexus is formed by anastomosis of three nerves, a median one arising from the posterior surface of the cerebral ganglia and a pair from the oesophageal commissures. Special nerves to the rectum are given off by the last abdominal ganglion.

Sense-Organs.—The paired eyes are well developed in the great majority of Decapods, although, as already mentioned, they may be reduced or entirely absent in deep-sea and cave-dwelling forms as well as in some parasitic and burrowing species. The cornea is generally distinctly faceted, the facets being square or hexagonal in outline. Sometimes they are square in the centre of the corneal area and hexagonal towards the margin. As a rule the crystalline cone is formed by four cells, and there are seven retinular cells enclosing a quadripartite rhabdome. The *nauplius-eye* has been found to persist in a vestigial condition in the adult in many of the lower Decapoda.

A pair of *statocysts* lodged in the proximal segment of the antennules occur in the great majority of Decapods (Fig. 156, A, *st*, p. 265). Only in certain Caridea do these organs appear to be entirely wanting (*Pandalus*, *Hippolyte*). The statocyst develops as an invagination of the integument, and in most of the lower Decapods it remains in communication with the exterior, sometimes by a wide aperture (*Crangon*), more commonly by a narrow slit. Rarely among the Natantia the statocyst appears to be quite closed (*Leucifer*, *Sergestes*), and this is the case also in the Galatheidea and Hippidea among the Anomura and in the whole of the Brachyura. In the Brachyura, after ecdysis, the statocyst is open to the exterior by a narrow slit, which, however, soon closes by coalescence of the newly formed cuticle covering its edges. In this group also the cavity assumes a complex form by the folding of its walls. In those cases where the statocyst remains open it contains a number of foreign particles, sand-grains, which act as statoliths, and are in some cases agglutinated together into a mass by an organic substance secreted by dermal glands on the inner surface of the sac. In this mass the tips of the sensory setae are embedded. When ecdysis takes place the chitinous cuticle lining the statocyst is thrown off and with it the contained sand-grains, and it has been shown that fresh grains are introduced by the animal either burying its head in the sand or placing the grains in position by means of its chelae. When the statocyst is without external opening it usually contains no solid particles.

This is the case in the Brachyura and the majority of the Anomura. In the few Natantia, however, which have closed statocysts, solitary statoliths, probably of organic composition, are present, which are no doubt formed *in situ*. As with the open statocysts, the lining membrane, and with it the statolith, is cast and renewed at each ecdysis. In all cases the inner surface of the statocyst bears plumose sensory setae arranged in one or more rows. In *Leucifer* the tips of the sensory hairs are embedded in the substance of the statolith.

The development of the statocysts has been traced in the Lobster and the Shore-crab. In both cases the functional state is assumed rather suddenly; at the fourth larval stage in the lobster and the first Megalopa-stage in the Crab. In the latter the statocyst is at first open to the exterior and sand-grains are found in it.

Sensory filaments occur in most cases on the external flagellum of the antennules, commonly in larger numbers in the male than in the female sex. In many Caridea they are confined to a specially thickened portion of the flagellum, and when the flagellum bifurcates the filaments are borne by the secondary branch (Fig. 156, B, p. 265). In some terrestrial species (*Coenobita*) the filaments are very short, forming a close fur.

Phosphorescent organs are now known in a number of deep-sea Decapoda (Sergestidae, Penaeidae, Hoplophoridae, Pandalidae, Eryonidae), but the nature of the organs differs widely in the different groups. In *Aristeus coruscans* (Penaeidae) (Fig 168) and *Heterocarpus alphonsi* (Pandalidae) (Fig. 148, p. 259) Alcock observed a luminous fluid to be emitted from the base of the antennae, apparently from the orifices of the antennal glands. This case may be compared with that of *Gnathophausia* among the Mysidacea, where a luminous secretion is produced by a gland on the maxilla which may possibly be the excretory maxillary gland. *Polycheles phosphorus* (Eryonidae) was found by the same observer to be "luminous at two points between the last pair of thoracic legs, where there is a triangular glandular patch." Numerous phosphorescent organs have been found by Coutière on the body and limbs of various Hoplophoridae, but their structure has not been examined. In *Sergestes challengeri* Hansen has found an extraordinary number of luminous organs (about 150) on the body and limbs, although they are not found in other species of the genus. In this case the structure recalls that found in the Euphausiacea. Each organ has, internally, a reflector, composed apparently of concentric lamellae, enclosing a mass of cells. There is nothing corresponding to the "striated body" of Euphausiacea, and the "lens" is double, the outer part being formed by a thickening of the cuticle which has no counterpart in the Euphausiacea.

Reproductive System.—The *testes* as a rule lie partly in the thoracic region and partly in the abdomen, and, except in some Paguridae, are connected with each other across the middle line. In the simplest cases, as in some Caridea, they are tubular in form, but as a rule they send off numerous caecal diverticula. In *Leucifer* the two testes unite with each other to form an unpaired mass lying below the intestine. In the Paguridae they are displaced backwards so as to lie wholly in the abdominal region, where they are unsymmetrically placed on the left side, either fused into a single mass or entirely separated from each other, the right testis lying in front of the left.

The vas deferens presents typically three divisions (which, however, are not distinctly defined in many Caridea): (1) a narrow

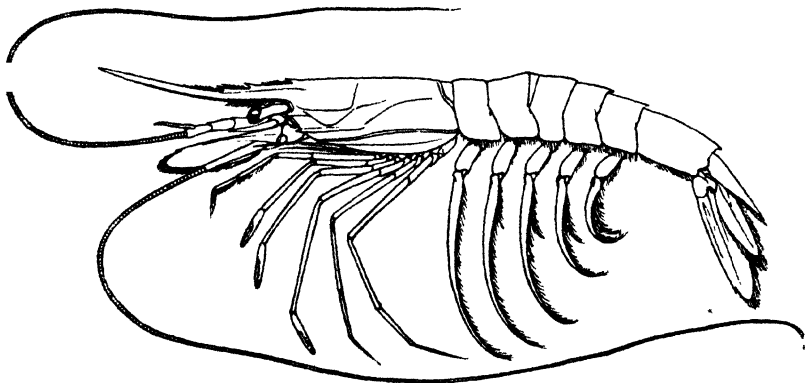


FIG. 168.
Aristeus coruscans (Penaeidae). (From Alcock, *Naturalist in Indian Seas*.)

efferent duct leading from the testis; (2) a glandular part, with wider lumen, often convoluted; (3) a terminal ductus ejaculatorius with muscular walls. In Brachyura (except Dromiidae) the distal portion of the second or glandular division is provided with caecal diverticula which in some cases are very numerous, forming a large glandular mass. In *Leucifer* the structure of the vas deferens is very complex, and there are two distinct glandular regions.

In nearly all cases the terminal portion of the vas deferens perforates the coxopodite of the last pair of legs, or emerges on the arthrodial membrane between the coxopodite and the body. In the majority of cases no penes are formed, but in some genera of Paguridae (*Spiropagurus*, etc.) a membranous tubular penis is present on one side only. In all Brachyura a pair of penes are present, the tips of which lie within the grooves of the first pair of abdominal appendages. In those families of Brachygnatha formerly

grouped together as Catometopa these penes either lie for a short distance from their base within grooves excavated in the last thoracic sternum, or else they perforate the sternum directly, the vasa deferentia in this case not entering the coxopodites of the legs at all, as they do in most other Decapods.

In most Macrura and in the Dromiidae the spermatozoa when discharged are enclosed by a sheath of secretion which sets to a firm membrane, forming a continuous cord-like mass. In *Scyllarus* and in the Anomura this is broken up into separate spermatophores attached by one end in a row on a strip of membrane. In the Brachyura (except the Dromiidae) the spermatophores are quite separate.

The spermatozoa are remarkably varied and complex in structure. As a rule they are provided with stiff radiating processes which serve to attach them to the surface of the egg, and, in some cases, an "explosive" apparatus is present which effects penetration of the egg-membrane.

The *ovaries* generally resemble the testes in shape and position. In the Penaeidae they may extend through the whole length of thorax and abdomen, but in most cases they are of less extent. In *Leucifer*, and in most if not all Thalassinidea and Paguridea, they lie wholly in the abdomen. They are always united across the middle line, sometimes at more than one point. In the Crayfish the two ovaries (like the testes) are joined together posteriorly so that the organ has a trilobed form. Except in *Leucifer* and in the Brachyura, the oviducts are simple in form and open on the coxopodites of the sixth thoracic appendages (third legs). In *Leucifer*, which is peculiar in so many points of structure, the oviducts have receptacula seminis connected with them and unite to open by a median aperture on the sternal surface of the thorax. In the Brachyura, where intromittent organs are developed in the male, the terminal part of the oviduct is of considerable length and serves as a vagina, while a lateral pouch, sometimes double, with glandular walls, forms a receptaculum seminis. In the Dromiacea the receptaculum seems to be a temporary structure formed at the time of copulation. In the Brachyura, with exception of the primitive Dromiacea and of certain Oxystomata (Raninidae, some Dorippidae), the oviducal apertures are removed from the coxopodites of the legs and open on the sternum of the corresponding somite.

In addition to the internal receptacula seminis mentioned above, an external organ having apparently the same function is found in certain Decapods. It is best known in the Penaeidae, where it has been named the *thelycum* and affords characters of systematic importance. It lies on the sternal surface of the thorax and appears to be formed by two or more outgrowths from the last

thoracic somite enclosing a cavity within which may sometimes be found the large foliaceous spermatophores deposited by the male. In the Lobster (*Homarus*) (Fig. 169) a median pouch enclosed by three processes on the sterna of the last two thoracic somites has the same function, and in the Crayfishes of the genus *Cambarus* (but not in *Astacus*) a more complicated organ in the same position is known as the "annulus ventralis." These structures have not hitherto been studied from a comparative point of view, but it seems likely that an investigation of their morphology and their relation to the structures occupying a similar position in the Syncarida would yield important results.

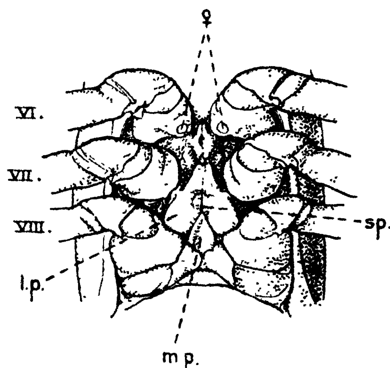


Fig. 169.

Sternal surface of posterior thoracic somites of female Lobster (*Homarus gammarus*), showing the receptaculum seminis. VI-VIII, bases of the last three pairs of legs; ♀, external openings of oviducts; *l.p*, lateral process on penultimate sternum; *m.p*, median process on last thoracic sternum; *sp*, slit-like opening of receptaculum.

In the great majority of Decapods the eggs after extrusion are carried by the female attached to the abdominal appendages. Only in the Penaeidea they appear to be shed free into the water immediately on extrusion, or carried for a short time only, as in *Leucifer*, where they have been found attached to the posterior thoracic limbs. The attachment of the eggs to the abdominal appendages of the parent is effected by means of a cementing material. As a rule this material seems to be produced by dermal glands, which are found abundantly developed on the inner faces of the pleural plates of the abdomen and on the uropods. In some cases (*Stenopus* and Thalassinidae), where the pleural plates are slightly developed, the glands occur mainly on the pleopods, and in the Paguridae they are distributed over the ventral integument of the abdomen. In the Brachyura, however, such glands are absent or only little developed, and the function of producing the cementing material is stated to be discharged by the receptaculum seminis.

Secondary sexual characters among the Decapods are numerous and varied. In many cases the males are distinguished from the females by the greater size and different shape of the chelipeds and by the narrower abdomen. Dimorphism of the males has been noted in many cases, and Faxon discovered that in Crayfishes of the genus *Cambarus* the two forms are alternating breeding and non-breeding phases in the life-history of the same individual. A closely similar series of changes has been found by Coutière and by

G. Smith in the males of some Oxyrhyncha, and it is very probable that it may occur also in other groups of Decapoda.

Mention may be made here of the remarkable phenomena of "parasitic castration," discovered by Giard in Decapods infested by Rhizocephala, Entoniscidae, and other parasites, and more recently investigated by G. Smith. The latter observer finds that, in Brachyura infected with *Sacculina*, the females show very little modification of external characters beyond a reduction in size of the pleopods, although the gonad is reduced in size or even completely eradicated. Infected males, however, assume in various degrees the secondary sexual characters proper to the female; the chelipeds (in species with dimorphic males) remain in the form of the non-breeding phase and resemble those of the female; the abdomen becomes more or less broadened and may assume completely the female form; the copulatory styles (first and second pleopods) are greatly reduced, and small pleopods may appear on the third to the fifth abdominal somites. In the most completely modified specimens only the reduced copulatory styles remain to show that they once were males. The very remarkable observation has been made that these completely modified males, in the rare cases when they recover sufficiently from the parasitic infection to regenerate a gonad, become perfect hermaphrodites, the gonad producing both spermatozoa and ova.

Observations, as yet unpublished, made by A. Wollebaek, seem to indicate that certain deep-water Decapoda are normally hermaphrodite.

Development.

With some noteworthy exceptions to be mentioned below, the Decapoda pass through a more or less extensive metamorphosis after leaving the egg. The most complete series of changes occurs among the Penaeidea, some at least of which are hatched as free-swimming nauplii and have a larval history closely parallel to that of the Euphausiacea.

In the Penaeidae the development was first made known by Fritz Müller, and further elucidated by Claus, Brooks, and Kishinouye. The *Nauplius* (Fig. 170, A), which has been hatched from the egg by the last-named of these authors, has a quite typical form. The pear-shaped or oval body is without a shell-fold and has two terminal setae posteriorly. The median eye is present and the three pairs of nauplius-limbs, the third pair of which are without any masticatory process. In the succeeding *Metanauplius*-stage four pairs of limb-rudiments are developed behind those already present, the masticatory process appears on the third pair, the swimming-branches of which begin to diminish, and a pair of papillae on the anterior margin represent the "frontal organs,"

which persist through several of the later stages. The next stage observed is the *Protozoea* (Fig. 170, B), in which the seven pairs of limbs already indicated are well developed; the carapace covers the anterior part of the body; the abdomen, which has a furcate termination, is still unsegmented, but the six posterior thoracic somites are defined, though very short. The mandibular palp has quite disappeared (to reappear at a later stage), and the first and second thoracic appendages are biramous swimming-limbs. At this stage the rudiments of the paired eyes begin to appear beneath the

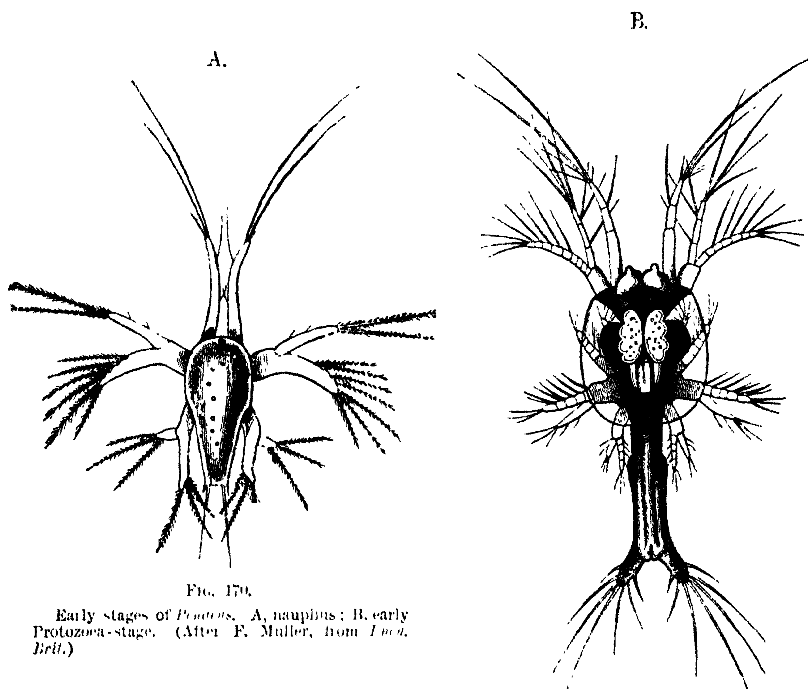


Fig. 170.

Early stages of *Penaeus*. A, nauplius; B, early Protozoea-stage. (After F. Muller, from *Encycl. Brit.*)

carapace, there are three pairs of hepatic caeca, and the heart is developed, though as yet with only one pair of ostia. In a later Protozoea-stage (Fig. 171, A) the five anterior abdominal somites are indicated, the sixth being not yet marked off from the telson, and the rudiments of the third pair of thoracic limbs appear. In the following stage, to which the name of *Zoea* is given, the paired eyes become free from the carapace and are movable, the carapace begins to grow out into a median rostral spine, the third pair of thoracic limbs are biramous, and rudiments of the remaining five pairs are present. The first five pairs of abdominal appendages (Fig. 171, B) are present as very small buds, but the sixth pair

have already begun to outstrip these in order of development and are larger and bilobed. In a later Zoea-stage (Fig. 171, C) the sixth pair form with the furcate telson a well-marked tail-fan, but the first five pairs of abdominal limbs are stated to be temporarily suppressed, to reappear again at a later stage; a retrograde change is also observed in the peduncle of the antennule, which in the later Protozoea was divided into five segments but now becomes

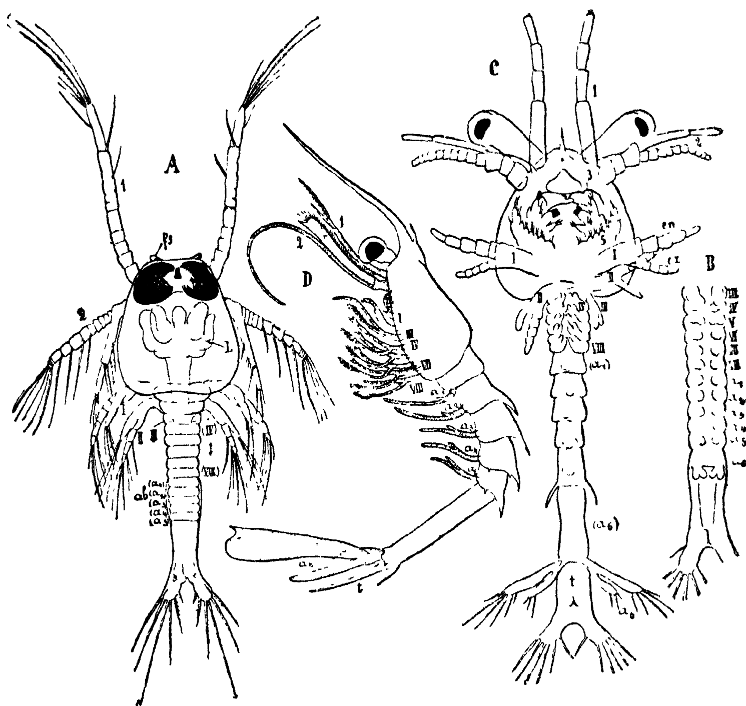


Fig. 171.

Later stages of *Penaeus*. A, older Protozoea-stage. B, under-surface of thorax and abdomen of somewhat later stage with rudiments of limbs. C, Zoea-stage. D, Schizopod-stage. 1, antennule; 2, antenna; 3, mandible; 4, maxillula; 5, maxilla; I-VIII, thoracic appendages; (IV-VIII), the posterior thoracic somites; a_1-a_5, pleopods; a_6, uropods; *ab*, abdomen; *en*, endopodite; *ex*, exopodite; *fr*, frontal sense-organ; *L*, hepatic caeca; *t*, telson. (After Claus, from Korschelt and Heider's *Embryology*.)

once more unsegmented. The five posterior pairs of thoracic limbs (legs), which in this stage are bilobed rudiments, develop in the succeeding *Schizopod*-stage (Fig. 171, D) (usually called the *Mysis*-stage) into biramous natatory limbs and take up the function of locomotion hitherto fulfilled chiefly by the antennae. The abdomen has now increased greatly in size as compared with the cephalothorax, and the first five pairs of abdominal appendages

begin to reappear. The various appendages now begin to assume the form which they have in the adult. The antennules have a three-segmented peduncle, with two flagella as yet unsegmented. The endopodite and exopodite of the antenna become respectively flagellum and scale. The palp of the mandible begins to redevelop. In a later stage, which may be called *post-larval*, the exopodites of the thoracic limbs become reduced and the abdominal appendages, now well developed, take on the function of swimming-organs.

While it is tolerably certain that the general course of development in the Penaeidae is as described above, it is to be observed that as yet the complete series of larval forms has not been traced out in the case of any one species, and it is just possible that some of the changes stated to occur, *e.g.* the alleged temporary disappear-

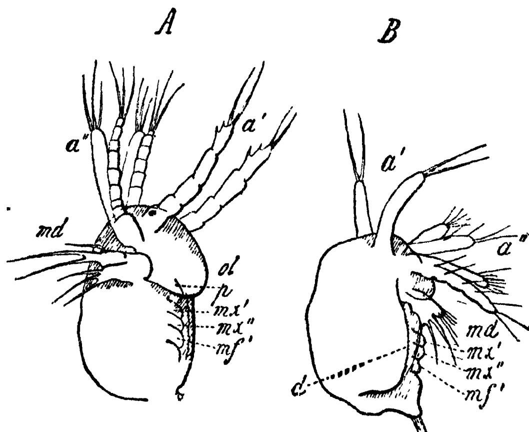


FIG. 172.

Metanauplius-stages of *Leucifer*. A, just hatched; B, later stage. *a′*, antennule; *a″*, antenna; *d*, shell-fold; *md*, mandible; *mf′*, first maxilliped; *mx′*, maxillula; *mx″*, maxilla; *ol*, labrum; *p*, paragnatha. (After Brooks, from Korschelt and Heider's *Embryology*.)

ance of the first five abdominal appendages in the later Zoea-stage, may be due to confusing together in one series the larvae of different species. In the closely related family of the Sergestidae, however, Brooks has been able to trace out in considerable detail the life-history of a single species, *Leucifer typus*. In this case the animal leaves the egg as a metanauplius (Fig. 172, A) with four pairs of limb-buds already visible behind the three pairs of nauplius-limbs. This is followed by a later metanauplius (Fig. 172, B) in which the shell-fold and the masticatory process of the mandible appear. The Protozoea (Fig. 173, A), with seven pairs of functional limbs, differs from that of *Penaeus* chiefly in the different shape of the carapace, which has already the beginning of a rostrum, and in having only four of the six posterior thoracic

somites defined. The rudiments of the paired eyes appear in the later Protozoea-stage (Fig. 173, D), when also the seventh thoracic

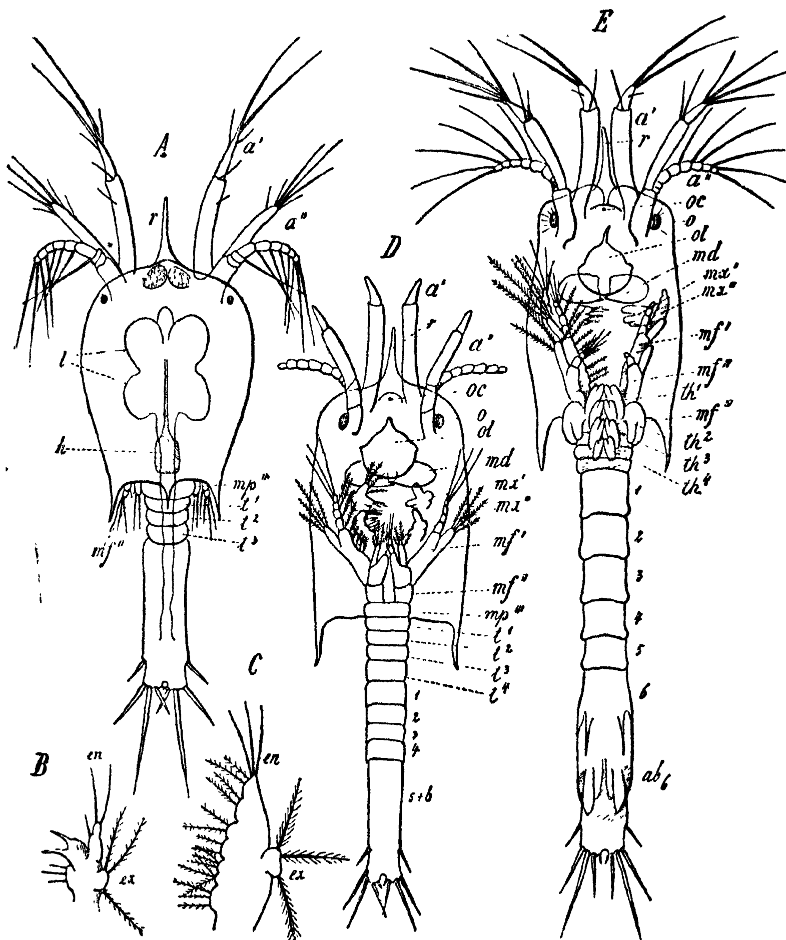


FIG. 173.

Protozoea and Zoea stages of *Leucifer*. A, first Protozoea-stage. B, maxillula of same. C, maxilla of same. D, later Protozoea-stage (*Erichthina*, Dana). E, Zoea-stage. *a'*, antennule; *a''*, antenna; ab_6, uropods; *en*, endopodite; *ex*, exite; *h*, heart; *l*, hepatic diverticula; *md*, mandible; *mf'*-*mf'''*, the three pairs of maxillipeds; *mp'''*, somite of third maxillipeds; *mx'*, maxillula; *mx''*, maxilla; *o*, paired eye; *oc*, nauplius-eye; *ol*, labrum; *r*, rostrum; th^1-th^4, rudiments of fourth to seventh thoracic limbs (first four legs); t^1-t^4, fourth to seventh thoracic somites; 1-6, abdominal somites. (After Brooks, from Korschelt and Heider's *Embryology*.).

somite (the eighth remains undeveloped in the adult *Leucifer*) and the first four abdominal somites appear. The Zoea-stage (Fig. 173, E) differs from that of *Penaeus* in the fact that the eyes are not

yet free from the carapace, and that the third thoracic limbs, like the four following pairs, only appear as bilobed rudiments. The uropods are present as rudiments, but the pleopods are not yet indicated. A Schizopod-stage (Fig. 174, A) follows, with movable paired eyes, with seven pairs of biramous thoracic appendages functioning as swimming-feet, and with well-developed tail-fan. Later stages (Fig. 174, B) show rudiments of the first five pleopods. A *Mastigopus*-stage (Fig. 174, C) intervenes before the assumption of the adult form.

The larvae of *Sergestes*, though differing remarkably in appearance from those of *Leucifer*, conform closely to the same type of development. The youngest known larvae are Protozoeae (Fig. 175, A), which differ from those of *Leucifer* in their compact form and in the possession of stalked eyes and of biramous third maxillipeds. The most characteristic feature, however, is the armature of the carapace. A rostrum, a median dorsal, and a pair of lateral spines are present as in *Leucifer*, but much stronger, and each bearing a double row of secondary spines. The Zoea (*Elaphocaris* of Dana) has this spine armature still more developed, and an additional pair of compound spines appear on either side of the rostrum. In the Schizopod-stage (known as *Acanthosoma*) (Fig. 175, B) the armature of the carapace is very much reduced. Before the adult stage is reached a *Mastigopus*-stage intervenes, characterised by the temporary disappearance of the last two pairs of thoracic limbs, which are present alike in the *Acanthosoma* and in the adult animal. It is interesting to notice that in this character *Leucifer* represents a permanent *Mastigopus*-form.

In the remaining groups of Decapoda no case is known where the larva is hatched at a stage preceding the Zoea, though in some instances a larval cuticle, moulted soon after hatching, has been supposed to present characters of the Protozoea.

Among the Caridea the earliest larval form is a Zoea in which the third thoracic appendages are already well developed. The posterior thoracic region is undeveloped, though the abdominal somites, with the exception of the last, are defined. The carapace has a rostrum and supra-orbital and antennal spines, but no further armature. In many cases the stage at hatching is still farther advanced, the paired eyes are stalked and movable, and one or more pairs of the posterior thoracic appendages are present as rudiments. In spite of the retarded development of the last five thoracic somites, it is noteworthy that the appendages appear in regular order from before backwards, with the exception of the uropods, which generally develop precociously. In the Schizopod-stage it is a very general but not universal character of the Caridean larva that it is without exopodites on the last thoracic feet. In many Caridea there is still further abbreviation, leading to complete suppression of the

larval stages, more especially among Arctic, abyssal, and freshwater forms. A specially interesting case is that of *Palaemonetes varians*,



FIG. 174.

Later stages of *Leucifer*. A, younger Schizopod-stage. B, later Schizopod-stage (less magnified). C, Mastigopus-stage. *a'*, antennule; *a''*, antenna; ab_1-ab_5, pleopods; ab_6, uropods; *c*, carapace; *dr*, antennal gland; *en*, flagellum, *ex*, scale, of antenna; *md*, mandible; *mf*, *mf''*, first and second maxillipeds; *mx'*, maxillula; *mx''*, maxilla; *o*, paired eye; *oc*, nauplius-eye; *ol*, labrum; *r*, rostrum; 1-6, abdominal somites. (After Brooks, from Korschelt and Heider's *Embryology*.)

of which two races are known, the one found in Southern Europe being exclusively freshwater in habitat; the other, found in Britain and Northern Europe, inhabiting brackish or salt water. The former hatches at a stage when all the limbs except the uropods are present, and the first two pairs of legs have exopodites. In

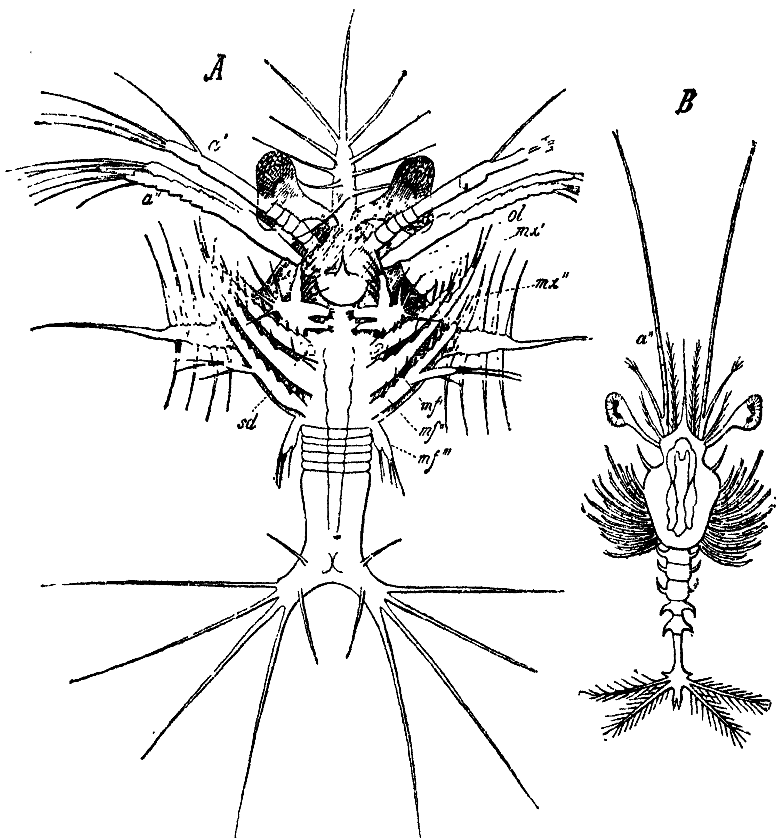


FIG. 175.

Larval stages of *Sergestes*. A, Protozoea-, B, Schizopod-stage (*Acanthosoma*). *a'*, antennule; *a''*, antenna; *mf'*-*mf'''*, the three pairs of maxillipeds; *mx'*, maxillula; *mx''*, maxilla; *ol*, labrum; *sd*, maxillary gland. (After Claus, from Korschelt and Heider's *Embryology*.)

the northern race all the ambulatory legs are rudimentary on hatching, and there are no abdominal limbs.

None of the Astacura are known to possess a Zoea-stage. The Lobster (*Homarus*) is hatched in the Schizopod-stage (Fig. 176), with natatory exopodites on all the thoracic limbs, but without any abdominal appendages. In the further course of development

the uropods are the last to appear. In *Nephrops* (Fig. 177) the course of development is very similar, but the larvae are distinguished by the long spines of the abdominal somites and telson. The freshwater Crayfishes have a direct development, the young on hatching resembling the adult in most points, but lacking the first and the last pairs of abdominal appendages.

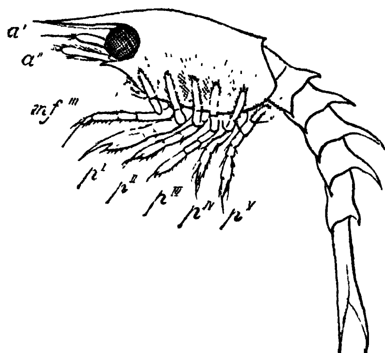


FIG. 176.

Larva of American Lobster (*Homarus americanus*), in Schizopod-stage. *a'*, antennule; *a''*, antenna; *mf'''*, third maxilliped; p^{i}-p^{v}, the five pairs of legs. (After S. I. Smith, from Korschelt and Heider's *Embryology*.)

The Scyllaridea have a very peculiar and characteristic series of larval forms, which were long described as adults under the generic name *Phyllosoma* (Fig. 178). These larvae are remarkable for the large size to which some attain, and for their extremely flattened and leaf-like form and glassy transparency. The body is sharply divided into three regions. The first, which is covered by the oval carapace, includes the head and the first two thoracic somites. The remainder of the thorax forms a discoidal plate and

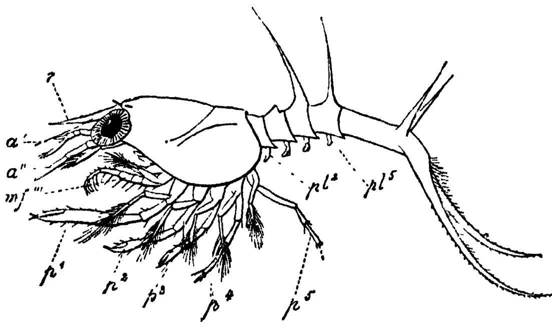


FIG. 177.

Late Schizopod-stage of *Nephrops norvegicus*. *a'*, antennule; *a''*, antenna; *mf'''*, third maxilliped; p^1-p^5, the five pairs of legs; pl^2, pl^5, pleopods; *r*, rostrum. (After Sars, from Korschelt and Heider's *Embryology*.)

is followed by the narrow and indistinctly segmented abdomen. The last two thoracic appendages are not developed in the newly hatched larva, but the four pairs in front of them are long and slender, with natatory exopodites. The first thoracic limbs are rudimentary (*Palinurus*) or absent (*Scyllarus*), and the second pair

are uniramous. It will thus be seen that the *Phyllosoma* represents a modification of an early Schizopod-stage.

A point of some interest in these forms is the occurrence of retrogressive changes in the course of development. Thus the antenna and the maxilla undergo a certain degree of degeneration before hatching, and the seventh and eighth thoracic and the abdominal somites, which are well defined in the embryo, become indistinct in the larva.

The development of Thalassinidea is interesting on account of the points of resemblance which it shows with the Caridea. The earliest larva is a Zoea, which in some cases (*Callianassa* and *Calocaris*) resembles that of Caridea in having the three maxillipeds

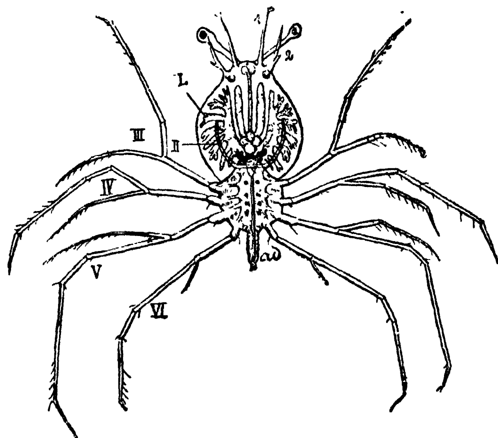


FIG. 178.

Phyllosoma-larva of *Palinurus*, just before hatching. *ad*, abdomen ; *L*, hepatic caeca ; II-VI, thoracic appendages (second and third maxillipeds and first three pairs of legs) ; 1, antennule ; 2, antenna. (After Claus, from Korschelt and Heider's *Embryology*.)

biramous and natatory ; but in others (*Upogebia* and *Jaxea*) only the first and second are present on hatching, the third becoming natatory only in the following Schizopod-stage, while the endopodite is still rudimentary, as in other Anomura. The existence of a Schizopod-stage, in which only the last two thoracic limbs are rudimentary and the uropods and rudiments of the pleopods are present, constitutes an important distinction from the other Anomura. The larvae of *Jaxea* (= *Calliaxis*) are of exceedingly peculiar form, having the cephalic region produced into a long "neck" resembling at first sight that of *Leucifer*. To this larval type the name of *Trachelifer* has been given. The remaining groups of the Anomura and the Brachyura differ from those just described in the suppression of the Schizopod-stage, the legs developing without exopodites in a *Metazoea*-stage which follows the Zoea. In the Anomura the Zoea

(Fig. 179, A) possesses two pairs of maxillipeds, the third pair (Fig. 179, C) being present as rudiments. The carapace has its posterior border produced into two lateral spines (greatly elongated in *Porcellana*, Fig. 180), and a long rostrum is present. In the next succeeding stage, the Metazoea (Fig. 179, B), the third maxilliped becomes biramous and natatory (a point of distinction from the Brachyuran type), and the uniramous ambulatory limbs and the pleopods are developed as rudiments.

The Brachyura, as a rule, are stated to hatch in the Zoea-stage (Fig. 181), but since rudiments of the posterior thoracic limbs are

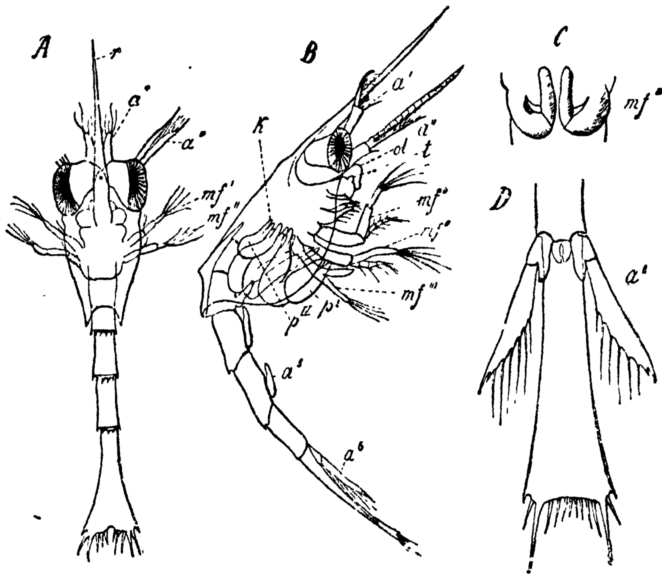


Fig. 179.

Larval stages of *Eupagurus bernhardus* (Paguridea). A, Zoea. B, Metazoea. C, rudiments of third maxillipeds in Zoea-stage. D, caudal fan of Metazoea. *a'*, antennule; *a''*, antenna; a^5, fifth pleopod; a^6, uropod; *k*, rudiments of gills; *mf'*-*mf'''*, the three pairs of maxillipeds; *ol*, labrum; p^{i}-p^{iv}, first four legs; *r*, rostrum; *t*, mandibular palp. (After Sars, from Korschelt and Heider's *Embryology*.)

frequently present, it might be more correct to call the larva a Metazoea. Throughout the group a very characteristic form is given to the Zoea by the development of long spines on the carapace. As a rule, a rostrum, a median dorsal, and a pair of lateral spines are present. Of these, the dorsal spine (*d.s*) is the most constant; great importance was formerly attached to it as a characteristic of the Zoea-stage. In many Brachyura the larva when hatched is enclosed in a cuticle which is moulted shortly after hatching, and this cuticle in many cases presents characters differing from those of the larva which escapes from it. In

Carcinus maenas, for instance, the first larval skin lacks the spines of the carapace, the antennae are larger and differently formed, the shape of the caudal fork and its spine armature are different from those of the succeeding stage, and the abdominal portion is not distinctly segmented. These characters have been supposed to indicate that we have here the last traces of a Protozoea-stage like that of the Penaeidea.

The Metazoeal stages, which differ from those of the Anomura in the fact that the third maxilliped does not assume a natatory function, are succeeded in nearly all cases by a *Megalopa*-stage (Fig. 182, A, B), in which all the appendages have assumed very much the form which they have in the adult, but the abdomen is large and usually carried extended, and the five pairs of pleopods are used for swimming. In some cases the Megalopa-stage is suppressed, the Metazoea being succeeded by a stage in which the animal has assumed the chief characters of the adult.

Complete suppression of the metamorphosis occurs in some (perhaps all) Potamonidae, and probably in some other freshwater and terrestrial Brachyura. In those Anomura which have become most completely terrestrial (*Birgus* and *Coenobita*) Borradaile has shown that the young are marine, and that hatching takes place at the Zoea-stage.



Fig. 180.

Metazoea of *Porcellana longicornis* (Galatheidea). *mf'*-*mf'''*, the three pairs of maxillipeds; *p*, rudiments of legs and gills. (After Sars, from Korschelt and Heider's *Embryology*.)

Remarks on Habits, etc.

The habits and habitats of the Decapoda are more varied, and have been much more studied, than in the case of any other group of Crustacea. Space will not permit of allusion to more than one or two of the more salient points.

Truly freshwater Decapods (apart from estuarine or brackish-water species which may penetrate into fresh water) are found among the Natantia in the family Atyidae and in several genera of Palaemonidae; of the Reptantia, the Crayfishes of the families Astacidae and Parastacidae, the monotypic Aegleidae among the Anomura, and the Potamonidae (Thelphusidae) and numerous species of Grapsidae among the Brachyura, are also dwellers in fresh water. Some of these are more or less amphibious in their habits, like many Potamonidae, and some Crayfishes are found burrowing in the earth far from streams or ponds, their burrows reaching down to the ground-water. The same is reported of the marine or brackish-water *Thalassina*.

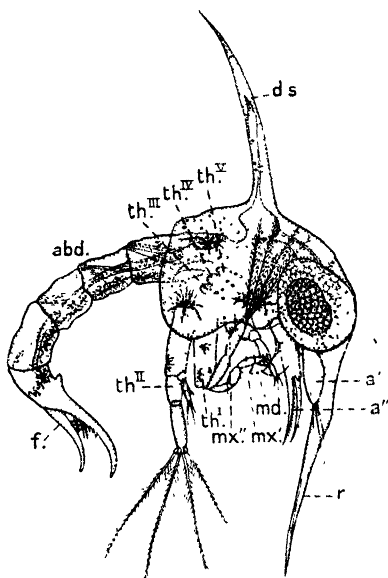


FIG. 181.

First Zoea-stage (after the first moult) of *Carcinus maenas*. *a'*, antennule; *a''*, antenna; *abd*, abdomen; *d.s*, dorsal spine of carapace (the so-called "Zoea"-spine); *f*, furcate telson; *md*, mandible; *mx'*, maxillula; *mx''*, maxilla; *r*, rostrum; *th*^{i}, *th*^{ii}, first and second maxillipeds, biramous and natatory; *th*^{iii}-*th*^{v}, rudiments of three following thoracic appendages. (After Faxon.)

Truly terrestrial species are found among Paguridae (*Birgus* and *Coenobita*) and Brachyura (Gecarcinidae), and it is interesting to note that these are derived not from freshwater but from marine types, and all (except, possibly, some Gecarcinidae) pass their early stages in the sea.

The Sergestidae belong to the plankton, occurring at the surface and descending to great depths. A few Brachyura (*Planes* and some other Grapsidae) lead a pelagic life, clinging to driftweed, floating timber, and the like.

It is worthy of note that the deep-sea Decapods include the more primitive members of each of the chief subdivisions: the Aristeinae among the Penaeidea, the Hoplophoridae among the Caridea, the Eryonidea among the Palinura, the Pylochelidae among the Paguridea, and the Homolodromiidae among the Brachyura.

Parasitism and commensalism in varying degrees are common. The Paguridae alone, which live in the empty shells of Gasteropod molluscs, present a whole series of cases of commensal association with Sponges, Coelentera (Fig. 183), and Polychaete worms;

Spongicola, *Typton*, and *Eiconaxius* live in sponges, many Pontoniinae and Pinnotheridae (as Aristotle knew) in the mantle-cavity of bivalve molluscs; members of the first-named family inhabit the pharyngeal cavity of Tunicates, and some Pinnotheridae are found in the "respiratory trees" of Holothurians and the rectum of sea-urchins. Many Decapods are constantly found among living corals, and the Hapalocarcinidae live in "galls" on the branches of corals. A very peculiar habit is that of some crabs of the genus *Melia*, which carry in each cheliped a living Actinian and use it as a weapon.

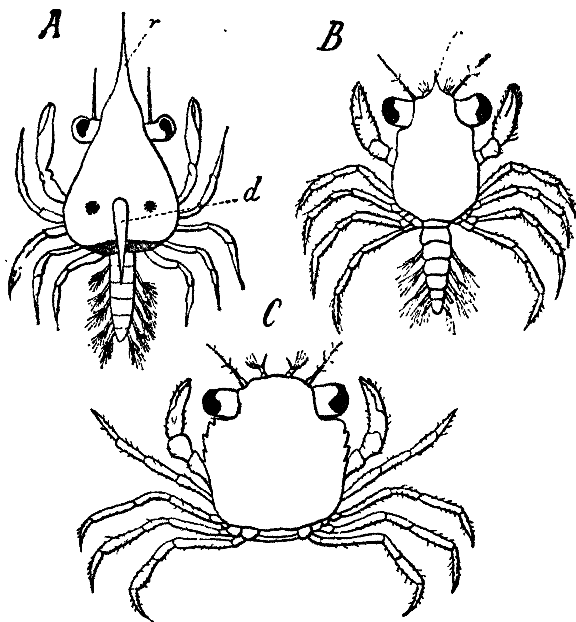


FIG. 182.

Later stages of *Carcinus maenas*. A, young Megalopa. B, older Megalopa. C, post-larval stage. *d*, dorsal spine of carapace; *r*, rostrum (A after Spence Bate; B and C after Brook. From Korschelt and Heider's *Embryology*.)

Special interest attaches to the stridulating organs, found in many Decapoda, since their possession is presumptive evidence that the animals do have some power of hearing. A few Penaeidae, some Palinuridae, and a considerable number of Brachyura are now known to have stridulating organs in various parts of the body. That of *Ocypoda*, shown in Fig. 184, is one of the few of which the sound-producing function has been demonstrated by observation of the living animals. It consists of a file-like series of ridges (*a*) on the inner surface of the propodite of one of the chelipeds, which can be rubbed up and down upon a sharp ridge (*b*) on the ischiopodite of the same appendage, producing a hissing sound, which probably

serves to warn intruders from entering the burrows of these shore-living crabs. In the case of purely aquatic species, the function of these organs is less easy to understand.

The range of size in Decapoda is greater than in any other group of Crustacea. Some Natantia do not exceed half an inch in length, one Pagurid is adult when 8 mm. long, a species of Porcellanid has a carapace measuring 3 mm. by 5 mm., and some Brachyura are no larger. The largest forms are found among the

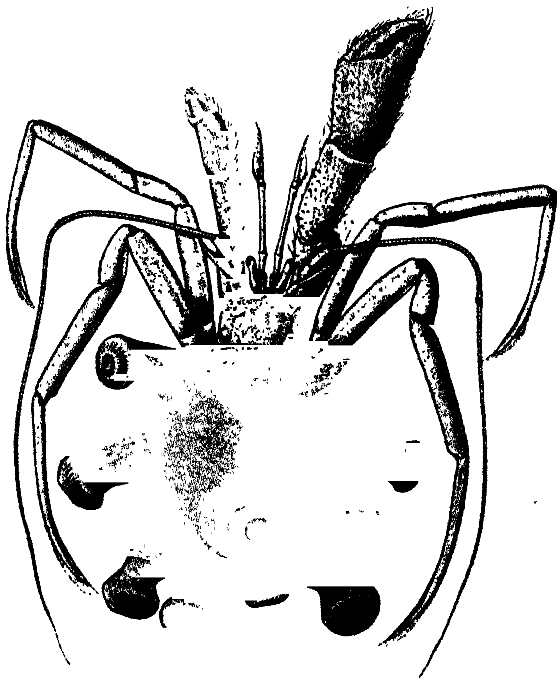


FIG. 183.

Parapagurus pilosimanus (Paguridae), lodged in a colony of zoantharian polypes. (From Alcock, *Naturalist in Indian Seas*.)

Reptantia; some Palinuridae and Astacura reach one or even two feet in length and are bulky in proportion. The largest living Arthropod is the Japanese crab *Macrocheira* (or *Kaempferia*) *Kaempferi*, of which the carapace may measure 15 inches in length, and the extended chelipeds of the male may span more than 10 feet.

PALAEONTOLOGY.

Fossil remains of Decapods are not known with certainty from any Palaeozoic deposits. Many genera from the Devonian upwards

have indeed been described as belonging to this group, but in no case is enough known of their characters to enable more to be said than that they agree with the "caridoid" groups of the Malacostraca in the possession of a carapace and of a tail-fan.

In the Mesozoic rocks many undoubted Decapods occur, including representatives of all the chief groups now living. Many genera of Penaeidea are found from the Jurassic, perhaps from the Triassic period onwards, some of the earliest even resembling closely the existing genus *Penaeus*, to which they have been referred. *Aeger*, from Triassic and Jurassic rocks, presents characters which suggest an affinity with the Stenopidea. True Caridea appear later, in the Upper Jurassic, some at least presenting primitive characters in the retention of exopodites on the ambulatory limbs. Freshwater Caridea of doubtful affinities occur in the Miocene. The Eryonidea are especially interesting since the few existing deep-

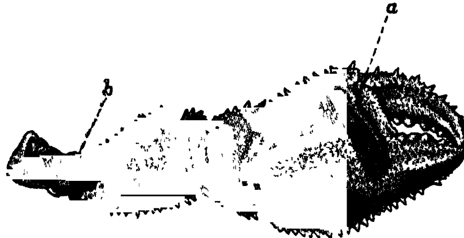


Fig. 184.

Larger cheliped of *Ocypoda macrocera*, from the inner side, showing the stridulating mechanism. *a*, tile-like series of ridges on propodite; *b*, ridge or scraper on ischiopodite against which the ridges of the propodite can be rubbed when the limb is flexed. (From Alcock, *Naturalist in Indian Seas*.)

sea forms appear to be only the surviving remnants of what was in the Mesozoic period a dominant group. The genus *Eryon* (Fig. 185) appears in the Trias and persists until the earlier Cretaceous. The Glyphaeidae, a wholly extinct group having much the same range in time as have the fossil Eryonidae, have been supposed to stand in the direct line of descent of the Scyllaridea. True Scyllaridea occur probably in the Jurassic, certainly in the Cretaceous period. The existing genus *Linuparus*, or a very close ally, dates back to the upper Chalk. Astacura are known from Jurassic and later deposits in considerable numbers. *Eryma*, from the Lias, and *Hoploparia* (Cretaceous and Tertiary) are well-known forms.

The Anomura are almost unknown as fossils, except for some Thalassinidea referred to the existing genus *Callianassa* occurring from the Upper Jurassic onwards. The Brachyura, on the other hand, are well represented. The earliest forms present characters of the Dromiacea, and are referred, for the most part, to the extinct family Prosoponidae, which Bouvier has shown to have close relations with the most primitive of existing Brachyura, the Homolo-

dromiidae. One of the oldest, and at the same time one of the most completely known, is *Palaeinachus* (Woodward) from the Forest Marble (Lower Oolite), which has many generalised characters. Later forms belonging to *Prosopon* (v. Meyer) and other genera give evidence, according to Bouvier, of the divergence of a Homoline and of a Dynomeno-Dromiine line of descent leading to such forms as

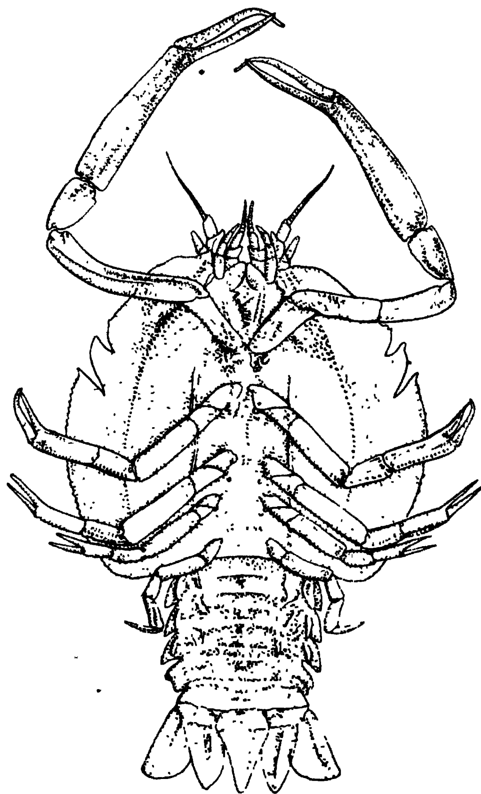


FIG. 185.

Eryon propinquus (from the Jurassic rocks of Solenhofen), under-side. (After Oppel.)

Homolopsis (Bell) and *Dromiopsis* (Reuss) from the Upper Cretaceous, and to the existing Homolidae, Dynomenidae, and Dromiidae. The remaining Brachyura have not yet yielded results of so much phylogenetic interest. The Oxystomata appear about the middle of the Cretaceous system and the Brachygnatha about the same time. In the Tertiary many Brachyura are found, representing the chief existing types of the group.

AFFINITIES AND CLASSIFICATION.

The resemblances between the lower Decapoda, especially the Penaeidea, and the Euphausiacea have been mentioned in dealing with the latter Order, and justify the alliance of the two Orders in the Division Eucarida. It may be mentioned that the exopodites of the thoracic legs, the absence of which still survives in text-books as distinguishing the Decapoda from the "Schizopoda," are at least as strongly developed in many Caridea (Hoplophoridae, etc.) (Fig. 160, p. 270) as in Euphausiacea or Mysidacea. Coutière has recently called attention to some curious resemblances between certain primitive Caridea and the Lophogastrid Mysidacea. These resemblances, however, by no means outweigh the important differences between the two groups, and may be either primitive characters derived from the common caridoid stock or convergences due to similarity of habits.

The classification of the Decapoda is a very difficult problem, and none of the schemes hitherto proposed can be regarded as entirely satisfactory. The traditional classification of the group into the long-tailed Macrura and short-tailed Brachyura was established by Latreille in 1806; but the difficulty of defining these groups is shown by the varying limits which have been assigned to the intermediate group of Anomura established by Milne-Edwards in 1834. Boas, in 1880, was the first to make a radical departure from this system. He pointed out that the Brachyura and Anomura were only single branches of the Decapod stock, and by no means equal in systematic value to the Macrura, which included several other branches not more closely connected with each other. In other words, just as in the classification of the Malacostraca as a whole, so within the Order Decapoda, the retention of the primitive "caridoid facies" does not necessarily imply close affinity between the groups exhibiting it. Boas proposed a division of the Order into the two primary groups of Natantia and Reptantia as defined below. This division is undoubtedly a more natural one than those formerly employed, although it is hardly more easy to find constant and exclusive structural characters by which to define the sub-orders than it was in the case of the Macrura, Anomura, and Brachyura. A further difficulty is presented by the small group of Stenopidea, which combine, to some extent, the characters of Natantia and Reptantia, and may perhaps deserve separation as a third sub-order. Important modifications of Boas's scheme have been introduced by Ortmann and by Borradaile, and the classification of the last-named author has been adopted here, with some alterations, chiefly of a formal kind, as, on the whole, the most satisfactory yet proposed. Borradaile's chief innovations are the inclusion of the Thalassinidea,

formerly ranked with the Macrura, among the Anomura, the establishment of a group Brachygnatha, opposed to the Dromiacea and Oxystomata among the Brachyura, and the abandonment of the old divisions Cyclometopa and Catometopa among the families which he unites as Brachyrhyncha. These changes appear to be quite justified on morphological grounds, and to conduce to clearness in the delimitation of the groups. Much work remains to be done, however, in readjusting the subdivisions of the smaller groups, and, in particular, the classification of the Caridea is still in a very unsatisfactory condition.

Although abandoned as a systematic category, the name Macrura may still be used (as it has been above) as a convenient descriptive term for those Decapoda which retain more or less the caridoid facies, that is to say, the Natantia with the Palinura and Astacura among the Reptantia.

With regard to many of the generic names mentioned below, it is necessary to warn the student that recent "reforms" of nomenclature have resulted in lamentable confusion, more especially in the naming of long-known and familiar Decapoda, and it is not safe to assume that when an author mentions "*Astacus*" or "*Crangon*" he is referring to the genera including the common Crayfish and the edible Shrimp.

ORDER **Decapoda**, Latreille (1802).

SUB-ORDER 1. **Natantia**, Boas (1880).

Body almost always laterally compressed ; rostrum usually compressed and serrated ; first abdominal somite not much smaller than the rest ; antennules generally with stylocerite ; antennal scale generally large and lamellar ; legs usually slender, exc[illegible] sometimes a stout chelate limb or pair, which may be any one of t[illegible]rst three pairs, with basipodite and ischiopodite very rarely coalesced and with only one fixed point in the carpo-propodal articulation (with some doubtful exceptions), sometimes with exopodites, podobranchiae hardly ever present on the first three and never on the last two pairs ; male genital apertures in articular membrane ; pleopods always present in full number, well developed, used for swimming.

TRIBE 1. PENAEIDEA.

Pleura of second abdominal somite not overlapping those in front ; antennae generally with stylocerite ; mandibular palps straight ; first maxillipeds without expansion at base of exopodite, endopodite long ; second maxillipeds with terminal segments normal ; third maxillipeds with seven segments ; third legs chelate (except when legs are much reduced), not stouter than first pair ; first pleopods of male with petasma ; gills dendrobranchiate.

Family PENAEIDAE. Sub-Family CERATASPINAE. *Cerataspis*, Gray.

Sub-Family ARISTEINAE. *Aristeus*, Duvernoy (Fig. 168, p. 289); *Benthesicymus*, Spence Bate. Sub-Family SICYONINAE. *Sicyonia*, H. Milne-Edwards. Sub-Family PENAEINAE. *Penaeus*, Fabricius; *Solenocera*, Lucas. Family SERGESTIDAE. Sub-Family SERGESTINAE. *Sergestes*, H. Milne-Edwards. Sub-Family LEUCIFERINAE. *Leucifer*, H. Milne-Edwards (= *Lucifer*, J. V. Thompson). [Sub-Family AMPHIONINAE. *Amphion*, H. Milne-Edwards. (The validity and the systematic place of this genus are still doubtful.)]

TRIBE 2. CARIDEA.

Pleura of second abdominal somite overlapping those in front; antennae generally with stylocerite; mandibular palp, if present, straight; first maxillipeds with expansion at base of exopodite, endopodite short; second maxillipeds usually with last segment articulating laterally with preceding; third maxillipeds with four to six segments; third legs never chelate; first pleopods of male without petasma; gills phyllobranchiate.

Family PASIPHAEIDAE. *Pasiphaea*, Savigny; *Psathyrocaris*, Wood-Mason (Fig. 160, p. 270). Family BRESILIIDAE. *Bresilia*, Calman. Family HOPLOPHORIDAE (ACANTHEPHYRIDAE). *Hoplophorus*, H. Milne-Edwards; *Acanthephyra*, A. Milne-Edwards. Family NEMATOCARCINIDAE. *Nematocarcinus*, A. Milne-Edwards. Family ATYIDAE. *Atya*, Leach; *Caridina*, H. Milne-Edwards; *Limnocaridina*, Calman. Family STYLODACTYLIDAE. *Stylodactylus*, A. Milne-Edwards. Family PSALIDOPODIDAE. *Psalidopus*, Wood-Mason and Alcock (Fig. 163, p. 272). Family PANDALIDAE. Sub-Family PANDALINAE. *Pandalus*, Leach; *Heterocarpus*, A. Milne-Edwards (Fig. 148, p. 259); *Pandalina*, Calman. Sub-Family THALASSOCARINAE. *Thalassocaris*, Stimpson. Family ALPHEIDAE. *Alpheus*, Fabricius; *Athanas*, Leach. Family HIPPOLYTIDAE. *Hippolyte*, Leach (= *Virbius*, Stimpson); *Spirontocaris*, Spence Bate; *Latreutes*, Stimpson. Family RHYNCHOCINETIDAE. *Rhynchocinetes*, H. Milne-Edwards. Family PALAEMONIDAE. Sub-Family PALAEMONINAE. *Palaemon*, Fabricius; *Palaemonetes*, Heller; *Leander*, Desmarest. Sub-Family PONTONIINAE. *Pontonia*, Latreille; *Typton*, Costa. Sub-Family HYMENOCERINAE. *Hymenocera*, Latreille. Family GNATHOPHYLLIDAE. *Gnathophyllum*, Latreille. Family PROCESSIDAE. *Processa*, Leach (*Nika*, Risso). Family GLYPHOCRANGONIDAE. *Glyphocrangon*, A. Milne-Edwards. Family CRANGONIDAE. *Crangon*, Fabricius; *Paracrangon*, Dana.

TRIBE 3. STENOPIDEA.

Pleura of second abdominal somite not overlapping those in front; antennae without stylocerite; mandibular palp curved inwards; first maxillipeds without expansion at base of exopodite, endopodite short; second maxillipeds with terminal segments normal; third maxillipeds with seven segments; third legs chelate, one or both much longer and stouter than first two pairs; first pleopods of male without petasma; gills trichobranchiate.

Family STENOPIDAE. *Stenopus*, Latreille; *Spongicola*, de Haan.

SUB-ORDER 2. **Reptantia**, Boas (1880).

Body not compressed, often depressed; rostrum often absent, depressed if present; first abdominal somite distinctly smaller than the rest; antennules without stylocerite; antennal scale generally small or absent; legs strong, the first pair usually, the others never, stouter than their fellows, basipodite and ischiopodite almost always coalesced in the first pair, generally also in the others, two fixed points in the carpo-propodal articulation, exopodites never present, podobranchiae often on some of the first four pairs; male genital apertures on coxopodites or on sternum; pleopods often reduced or absent, not used for swimming.

SECTION 1. PALINURA.

Abdomen extended, well-armoured, with well-developed pleura and broad tail-fan; carapace fused at sides with epistome; rostrum generally small or absent; exopodites of maxillipeds with flagella directed forwards; third legs like the first, chelate or simple; appendix interna present on some pleopods, at least in female; exopodites of uropods not distinctly segmented; branchiae numerous.

TRIBE 1. ERYONIDEA.

Antennae with exopodite, first segment not fused with epistome; first four pairs or all the legs chelate; first pleopods present.

Family ERYONIDAE. *Polycheles*, Heller; *Pentacheles*, Spence Bate (Fig. 162, p. 271); *Eryon*, Desmarest (Fossil) (Fig. 185, p. 308).

TRIBE 2. SCYLLARIDEA.

Antennae without exopodite, first segment fused with epistome; none of the legs chelate except sometimes the last pair in the female; first pleopods absent.

Family PALINURIDAE. *Palinurus*, Fabricius; *Linuparus*, White; *Palinurellus*, von Martens. Family SCYLLARIDAE. *Scyllarus*, Fabricius; *Ibacus*, Leach; *Thenus*, Leach.

SECTION 2. ASTACURA.

Abdomen as in Palinura; carapace not fused at sides with epistome; rostrum well developed; exopodites of maxillipeds as in Palinura; first three pairs of legs chelate; no appendix interna on pleopods; exopodites of uropods divided by a suture; branchiae numerous.

TRIBE NEPHROPSIDEA.

Family NEPHROPSIDAE. *Nephrops*, Leach; *Nephropsis*, Wood-Mason (Fig. 161, p. 270); *Homarus*, H. Milne-Edwards. Family PARASTACIDAE. *Parastacus*, Huxley; *Paranephrops*, White. Family ASTACIDAE. *Astacus*, Fabricius (*Potamobius*, Samouelle); *Cambarus*, Erichson.

SECTION 3. ANOMURA.

Abdomen rarely as in Palinura, generally soft, or bent upon itself, pleura generally small or absent, tail-fan often reduced ; carapace not fused with epistome ; exopodites of maxillipeds with flagella, when present, bent inwards ; third legs unlike the first, never chelate ; appendix interna sometimes present ; uropods rarely absent ; exopodites sometimes segmented ; branchiae few.

TRIBE 1. GALATHEIDEA.

Abdomen bent upon itself, symmetrical ; body depressed ; rostrum often well developed ; first legs chelate ; tail-fan well developed.

Family AEGLEIDAE. *Aeglea*, Leach. Family UROPTYCHIDAE. *Uroptychus*, Henderson ; *Chirostylus*, Ortmann. Family GALATHEIDAE. Sub-Family GALATHEINAE. *Galathea*, Fabricius ; *Munida*, Leach (Fig. 150, p. 260). Sub-Family MUNIDOPSINAE. *Munidopsis*, Whiteaves. Family PORCELLANIDAE. *Porcellana*, Leach ; *Petrolisthes*, Stimpson.

TRIBE 2. THALASSINIDEA.

Abdomen extended, symmetrical ; body compressed ; rostrum sometimes well developed ; first legs chelate, rarely sub-chelate ; tail-fan well developed.

Family AXIIDAE. *Axius*, Leach (including *Eiconaxius*, Spence Bate, and *Iconaxiopsis*, Alcock (Fig. 149, p. 260), as subgenera) ; *Calocaris*, Bell. Family LAOMEDIIDAE. *Laomedia*, de Haan ; *Jaxea*, Nardo. Family CALLIANASSIDAE. Sub-Family CALLIANASSINAE. *Callianassa*, Leach ; *Callianidea*, H. Milne-Edwards. Sub-Family UPOGEBIINAE. *Upogebia*, Leach (= *Gebia*, Leach). Family THALASSINIDAE. *Thalassina*, Latreille.

TRIBE 3. PAGURIDEA.

Abdomen nearly always asymmetrical, either soft and twisted or bent under thorax ; rostrum generally small or absent ; first legs chelate ; tail-fan not typical, uropods (when present) adapted for holding the body into hollow objects.

Family PYLOCHELIDAE. *Pylocheles*, A. Milne-Edwards (Fig. 151, p. 261). Family PAGURIDAE. Sub-Family PAGURINAE. *Pagurus*, Fabricius ; *Clibanarius*, Dana. Sub-Family EUPAGURINAE. *Eupagurus*, Brandt ; *Spiropagurus*, Stimpson ; *Parapagurus*, S. I. Smith (Fig. 183, p. 306). Family COENOBITIDAE. *Coenobita*, Latreille ; *Birgus*, Leach (Fig. 152, p. 262). Family LITHODIDAE. Sub-Family LITHODINAE. *Lithodes*, Latreille ; *Neolithodes*, Milne-Edwards and Bouvier (Fig. 153, p. 262). Sub-Family HAPALOGASTRINAE. *Hapalogaster*, Brandt.

TRIBE 4. HIPPIDEA.

Abdomen bent under thorax, symmetrical ; rostrum small or absent ; first legs styliform or sub-chelate ; tail-fan not adapted for swimming.

Family ALBUNEIDAE. *Albunea*, Fabricius. Family HIPPIDAE. *Hippa*, Fabricius ; *Remipes*, Latreille.

SECTION 4. BRACHYURA.

Abdomen small, symmetrical, bent under thorax, tail-fan not developed ; carapace fused with epistome at sides and nearly always in the middle ; exopodites of maxillipeds with flagella, when present, bent inwards ; first legs always, third legs never, chelate ; no appendix interna on pleopods ; uropods rarely present, never biramous ; branchiae generally few.

TRIBE 1. DROMIACEA.

Last pair of legs modified, dorsal in position ; female openings on coxopodites ; first pleopods present in female ; branchiae sometimes numerous ; mouth-frame quadrate.

SUB-TRIBE 1. DROMIIDEA.

Sternum of female with longitudinal grooves ; vestiges of uropods usually present ; branchiae 14-20 on each side ; eyes completely sheltered by orbits ; no linea homolica on carapace.

Family HOMOLODROMIIDAE. *Homolodromia*, A. Milne-Edwards. Family DROMIIDAE. *Dromia*, Fabricius. Family DYNOMENIDAE. *Dynomene*, Latreille.

SUB-TRIBE 2. HOMOLIDEA.

Sternum of female without longitudinal grooves; no uropods ; branchiae 8-14 on each side ; eyes not completely sheltered by orbits ; linea homolica usually present on carapace.

Family HOMOLIDAE. *Homola*, Leach. Family LATREILLIIDAE. *Latreillia*, Roux.

TRIBE 2. OXYSTOMATA.

Last pair of legs normal or modified ; female openings generally on sternum ; first pleopods wanting in female ; branchiae few ; mouth-frame triangular, produced forwards over epistome.

Family DORIPPIDAE. *Dorippe*, Fabricius ; *Ethusa*, Roux ; *Cyclodorippe*, A. Milne-Edwards. Family RANINIDAE. *Ranina*, Lamarck. Family CALAPPIDAE. Sub-Family CALAPPINAE. *Calappa*, Fabricius. Sub-Family ORITHYINAE. *Orithya*, Fabricius. Sub-Family MATUTINAE. *Matuta*, Fabricius. Family LEUCOSIIDAE. Sub-Family LEUCOSIINAE. *Leucosia*, Fabricius ; *Ebalia*, Leach. Sub-Family ILIINAE. *Ilia*, Leach.

TRIBE 3. BRACHYGNATHA.

Last pair of legs normal, rarely reduced or dorsal in position ; female openings on sternum ; first pleopods wanting in female ; branchiae few ; mouth-frame quadrate.

SUB-TRIBE 1. BRACHYRHYNCHA.

Body not narrowed in front ; rostrum reduced or wanting ; orbits well formed.

Family CORYSTIDAE. *Corystes*, Latreille. Family PORTUNIDAE. Sub-Family CARCININAE. *Carcinus*, Leach (*Carcinides*, Rathbun). Sub-Family PORTUMNINAE. *Portumnus*, Leach. Sub-Family CATOPTRINAE. *Catoptrus*, A. Milne-Edwards. Sub-Family CARUPINAE. *Carupa*, Dana. Sub-Family PORTUNINAE. *Portunus*, Fabricius. Sub-Family CAPHYRINAE. *Caphyra*, Guérin. Sub-Family THALAMITINAE. *Thalamita*, Latreille. Sub-Family PODOPHTHALMINAE. *Podophthalmus*, Lamarck. Family POTAMONIDAE. Sub-Family DECKENIINAE. *Deckenia*, Hilgendorf. Sub-Family PSEUDOTHELPHUSINAE. *Pseudothelphusa*, Saussure. Sub-Family POTAMONINAE. *Potamon*, Savigny (= *Thelphusa*, Latreille). Sub-Family TRICHODACTYLINAE. *Trichodactylus*, Latreille. Family ATELECYCLIDAE. Sub-Family ACANTHOCYCLINAE. *Acanthocyclus*, Milne-Edwards and Lucas. Sub-Family THIINAE. *Thia*, Leach. Sub-Family ATELECYCLINAE. *Atelecyclus*, H. Milne-Edwards. Family CANCRIDAE. Sub-Family CANCRINAE. *Cancer*, Linnaeus. Sub-Family PIRIMELINAE. *Pirimela*, Leach. Family XANTHIDAE. Sub-Family XANTHINAE. *Xantho*, Leach. Sub-Family CARPILIINAE. *Carpilius*, Leach. Sub-Family ETISINAE. *Etisus*, H. Milne-Edwards. Sub-Family MENIPPINAE. *Menippe*, de Haan. Sub-Family OZIINAE. *Ozius*, H. Milne-Edwards. Sub-Family ERIPHIINAE. *Eriphia*, Latreille. Sub-Family TRAPEZIINAE. *Trapezia*, Latreille. Family GONOPLACIDAE. Sub-Family RHIZOPINAE. *Rhizopa*, Stimpson. Sub-Family PRIONOPLACINAE. *Prionoplax*, H. Milne-Edwards. Sub-Family GONOPLACINAE. *Gonoplax*, Leach. Sub-Family CARCINOPLACINAE. *Carcinoplax*, H. Milne-Edwards. Sub-Family HEXAPODINAE. *Hexapus*, de Haan. Family PINNOTHERIDAE. Sub-Family PINNOTHERINAE. *Pinnotheres*, Latreille. Sub-Family PINNOTHERELIINAE. *Pinnotherelia*, Milne-Edwards and Lucas. Sub-Family XENOPHTHALMINAE. *Xenophthalmus*, White. Sub-Family ASTHENOGNATHINAE. *Asthenognathus*, Stimpson. Family PTENOPLACIDAE. *Ptenoplax*, Alcock and Anderson. Family PALICIDAE. *Palicus*, Philippi (= *Cymopolia*, Roux). Family GRAPSIDAE. Sub-Family PLAGUSIINAE. *Plagusia*, Latreille. Sub-Family SESARMINAE. *Sesarma*, Say. Sub-Family GRAPSINAE. *Grapsus*, Lamarck ; *Planes*, Bowdich (= *Nautilograpsus*, H. Milne-Edwards). Sub-Family VARUNINAE. *Varuna*, H. Milne-Edwards. Family GECARCINIDAE. *Gecarcinus*, Leach ; *Cardisoma*, Latreille. Family OCYPODIDAE. Sub-Family MACROPHTHALMINAE. *Macrophthalmus*, Latreille. Sub-Family OCYPODINAE. *Ocypoda*, Fabricius (Fig. 155, p. 264) ; *Gelasimus*, Latreille. Sub-Family MYCTIRINAE. *Myctiris*, Latreille. Family HAPALOCARCINIDAE. *Hapalocarcinus*, Stimpson.

SUB-TRIBE 2. OXYRHYNCHA.

Body narrowed in front ; rostrum usually distinct ; orbits generally incomplete.

Family HYMENOSOMIDAE. *Hymenosoma*, Desmarest. Family MAIIDAE. Sub-Family INACHINAE. *Inachus*, Fabricius; *Macrocheira*, de Haan; *Macropodia*, Leach. Sub-Family ACANTHONYCHINAE. *Acanthonyx*, Latreille. Sub-Family PISINAE. *Pisa*, Leach; *Hyas*, Leach. Sub-Family MAIINAE. *Maia*, Lamarck (= *Mamaia*, Stebbing); *Pericera*, Latreille; *Mithrax*, Leach. Family PARTHENOPIDAE. Sub-Family PARTHENOPINAE. *Parthenope*, Fabricius; *Lambrus*, Leach. Sub-Family EUMEDONINAE. *Eumedonus*, H. Milne-Edwards.

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CHAPTER XVI

THE STOMATOPODA

Division Hoplocarida.

Order **Stomatopoda**, Latreille (1817).

For a definition of the Division Hoplocarida, see p. 149.

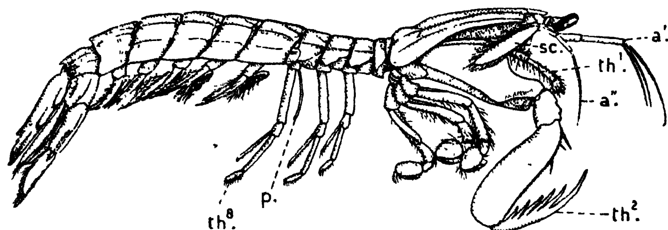
Historical.—The common and conspicuous *Squilla mantis* of the Mediterranean can hardly have escaped notice in antiquity, and it is surprising that it cannot be identified with certainty among the Crustacea mentioned by Aristotle. It was described by Rondelet (1555) under the generic name which it still bears. The group Stomatopoda, as defined by Latreille in 1817, had practically the limits now assigned to it, though some larvae were admitted to generic rank along with the adults. By H. Milne-Edwards the group was extended to include not only the "Schizopoda," but also some larval and adult Decapods (*Phyllosoma*, *Leucifer*, etc.). Restricted by subsequent writers to the single family Squillidae, the Order has generally been ranked along with "Schizopoda" and Decapoda in the group Podophthalma, though Huxley and, later, Grobben have pointed out the great differences separating the Stomatopoda from the other stalk-eyed groups.

The first details as to the larval metamorphosis of the Order were given by F. Müller (1862-64). Claus, in a remarkable memoir (1871), traced out several developmental series. Later workers, especially Brooks (1886) and Hansen (1895), have succeeded in referring many larvae to the various genera and species of adults. It is to be noted, however, as Hansen has pointed out, that the number of specific forms among the larvae exceeds that of the known adult species.

Morphology.

The general appearance of the Stomatopoda is highly characteristic and very constant throughout the group. Its most striking features are due to the great development of the abdominal region and its appendages, the small size of the carapace, and the large and peculiarly formed raptorial limbs.

The body (Fig. 186) is more or less flattened dorso-ventrally. The carapace is fused dorsally with at least two of the thoracic somites, two others are represented by indistinct vestiges overlapped by its hinder edge, while the last four are free and completely developed. The lateral wings of the carapace project more or less horizontally, roofing over on each side a widely open channel



Squilla mantis, male, from the side. *a'*, antennule; *a''*, antenna; *p*, penis; *sc*, scale or exopodite of antenna; *th*1, *th*2, *th*8, first, second, and last thoracic appendages.

within which lie the epipodites of the anterior thoracic appendages, and which corresponds to the branchial cavity of other forms. Anteriorly the carapace does not extend to the front of the head (Fig. 187), leaving uncovered two movably articulated segments,

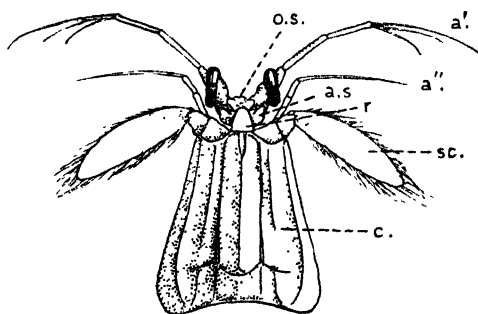


FIG. 187.

Anterior part of body of *Squilla mantis*, from above. *a'*, antennule; *a''*, antenna; *a.s*, antennular segment of head; *c*, carapace; *o.s*, ophthalmic segment of head; *r*, rostral plate; *sc*, scale or exopodite of antenna.

which carry respectively the eyes and the antennules, and which are commonly regarded as representing the ocular (*o.s*) and antennular (*a.s*) somites. A small rostral plate (*r*), movably articulated with the front edge of the carapace, overlies the antennular segment.

That part of the head lying between the point of attachment of the antennae and that of the mandibles is much elongated, forming

a narrow "neck," which, except for the lateral wings of the carapace projecting on either side, recalls the similarly formed "neck" of *Leucifer* and of the *Trachelifer*-larva of *Jaxea*. The anterior thoracic somites are much abbreviated and crowded together. The first and second are apparently not distinct from the carapace in the adult. The third and fourth are at most represented dorsally by small sclerites overlapped by the hinder part of the carapace. The fifth and succeeding thoracic somites are complete, and movably articulated. The abdominal somites often increase in width posteriorly, and their horizontally extended pleural plates may become greatly expanded in certain species.

The telson (Fig. 188, *t*) is very broad and its posterior margin is generally cut into sharp teeth; it is firmly united to the preceding somite in certain species of *Gonodactylus* (*Protosquilla*, Brooks).

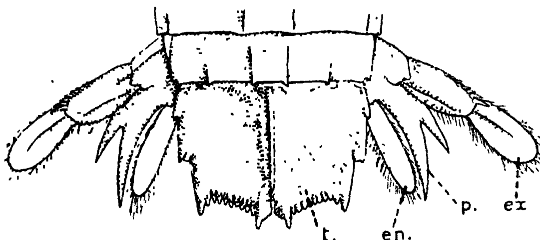


FIG. 188.
Caudal fan of *Squilla mantis*, upper surface. *en*, endopodite; *ex*, exopodite; *p*, process from peduncle of uropod; *t*, telson.

The surface of the carapace and of the body-somites is often ornamented with longitudinal keels, and the telson is always more or less elaborately sculptured.

Appendages.—The *antennules* (Fig. 187, *a′*) have an elongated peduncle of three segments, which bears three comparatively short flagella. Of these, the two on the outer side spring from a common stalk which is unsegmented; the inner flagellum is also unsegmented for a short distance from its base.

The *antennae* (Fig. 187, *a″*) have a protopodite of two segments, a large exopodite, and a comparatively feeble endopodite. The exopodite consists of a small basal segment and an oval membranous scale (*sc*) with setose margins; the endopodite has two elongated proximal segments and a short flagellum.

The *mandibles* (Fig. 189, A) carry a slender palp of three segments. The oral edge is crescentic and strongly serrate, its two cornua corresponding respectively to the incisor and molar processes of other Malacostraca. The proximal cornu projects upwards into the cavity of the mouth.

The *maxillulae* (Fig. 189, B) have two endites, the distal

one terminating in a strong curved spine. A vestigial palp is present (*p*).

The *maxillae* (Fig. 189, C) have a peculiar and characteristic form which cannot be closely compared with that of the corresponding appendage in other Malacostraca. They appear to consist of four segments, of which the first and second are indistinctly separated.

The first five pairs of *thoracic appendages* are similar in structure and are commonly called maxillipeds, though, as they possess no endites or other adaptations for mastication, the name is hardly appropriate. Each consists of only six segments (there is no evidence to show how these are related to the seven segments commonly recognised in other Malacostraca) and terminates in a

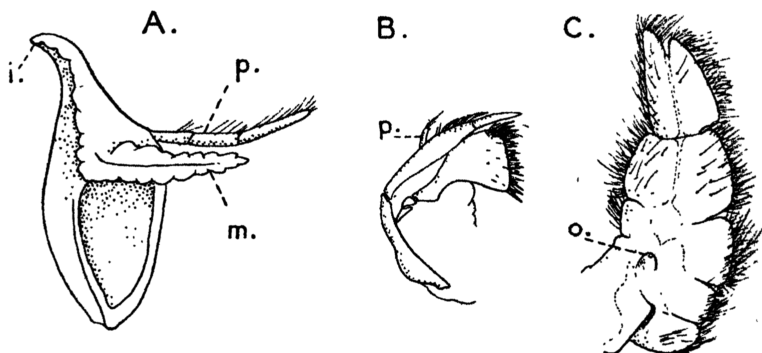


Fig. 189.

Mouth-parts of *Squilla mantis*. A, mandible, seen from the inner, or oral, side; B, maxillula; C, maxilla. *i*, incisor process; *m*, molar process; *o*, papilla bearing opening (of maxillary gland ?); *p*, palp.

prehensile "hand" or sub-chela; there are no exopodites, but epipodites (Fig. 190, A, *ep*) are present on all five pairs in the form of discoid membranous plates or vesicles attached to the basal segment by a narrow neck. The first pair of limbs (Fig. 190, A) are long and slender and the terminal segment is minute; the second pair are very massive, forming powerful weapons (Fig. 186, th^2); the third, fourth, and fifth pairs resemble each other and are less powerful. In each case the terminal segment is flexed upon the preceding one in such a way that its point is directed forwards, an arrangement which recalls the peculiar inverted chela of the Amphipod *Trischizostoma*. The last three pairs of thoracic limbs (Fig. 186, th^8) are slender, biramous, and without epipodites. The protopodite is very distinctly composed of three segments, of which the second is elongated. The inner (and anterior) of the two rami is the stouter and consists of two segments; the outer is slender and unjointed. According to Claus, the development of

the limb shows the outer branch to be the endopodite and the inner the exopodite, the relative positions of the two being reversed in the course of development.

The *pleopods* (Fig. 190, B, C) are remarkable in carrying the branchial apparatus. The broad and flattened protopodite has articulated with it at some distance from each other the endopodite and exopodite, each of which is lamellar and membranous and is obscurely divided into two segments. From the inner edge of the endopodite springs a short appendix interna (*i*), bearing a group of coupling-hooks. The branchiae (*br*) consist of a main stem springing from the anterior face of the exopodite near its base, extending horizontally inwards, and carrying on its lower edge a

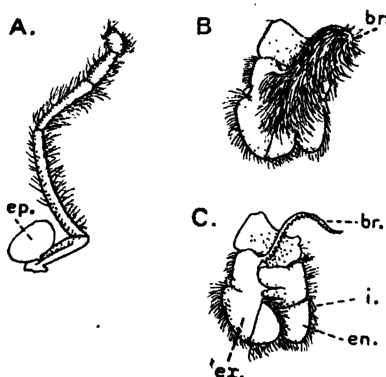


FIG. 190.

A, first thoracic appendage of *Squilla mantis*. B, second pleopod, showing the branchial appendage. C, the same, after removal of the branchial filaments. *br*, branchial appendage; *en*, endopodite; *ep*, epipodite; *ex*, exopodite; *i*, appendix interna.

series of tufts of ramified branchial filaments. In the female all the pleopods are similar, but in the male the first pair have the endopodite modified.

The *uropods* form, with the telson, a broad tail-fan (Fig. 188). The short protopodite runs out into a flattened plate (*p*) lying between and below the rami, divided distally into two sharp teeth. The exopodite is distinctly divided into two segments.

Alimentary System.—The stomach is large and thin-walled and is divided into two chambers. Its armature is slightly developed as compared with that of most Decapods. The anterior or cardiac chamber is large and extends in front of the mouth as far as the base of the rostrum. In its posterior wall lie two pairs of rod-like sclerites, the upper pair articulating with an unpaired plate which forms the floor of the smaller pyloric chamber and projects as a median keel into its cavity. The intestine is very narrow, but expands somewhat at about the fifth abdominal somite to form the

rectum. A pair of glandular sacs lying in the telson on either side of the anus have been observed in the larva and perhaps open into the rectum. It is not known whether they persist in the adult.

The digestive gland is very voluminous. It forms a compact mass of glandular tissue closely investing the intestine throughout the whole of its length and sending out on each side a series of diverticula segmentally arranged corresponding to the last three thoracic and the abdominal somites, and it finally terminates in a series of ramifying processes, which radiate throughout the telson and even penetrate into the peduncles of the uropods. It was formerly stated that this gland originated as a series of segmentally arranged diverticula from the alimentary canal, and that it communicated with the intestine by a series of apertures on each side throughout its whole length. It appears, however, that this is not the case, but that the gland-follicles open into a pair of longitudinal ducts which unite to enter the dorsal part of the pyloric chamber of the stomach.

Circulatory System.—The Stomatopoda are unique among the Eumalacostraca in possessing an elongated tubular heart extending through nearly the whole length of the thoracic and abdominal regions, and provided with numerous segmentally arranged pairs of ostia.

The details of the circulatory system have been most fully made out in the later larval stages by Claus, but the older accounts of the adult by Audouin and Milne-Edwards and by Duvernoy, though incomplete, show that no very profound changes occur in the adult. The anterior part of the tubular heart, lying in the maxillary region, is dilated, and its dorsal wall is perforated by a pair of large ostia. Anteriorly, it gives off a median aorta which sends branches to brain, eyes, antennules, and antennae, and a pair of antero-lateral arteries to the carapace and viscera. Behind the region of the first thoracic appendages the heart is of uniform diameter, and bears twelve pairs of ostia and fourteen pairs of lateral arteries arranged for the most part in correspondence with the segmentation of the body. Posteriorly the heart is continued into a short caudal aorta running into the telson.

From one of the lateral arteries of the first pair there originates an unpaired arteria descendens, which pierces the ventral ganglionic mass between the first and second thoracic ganglia, to communicate with a subneural artery which underlies the nerve-cord throughout its whole length. This subneural artery further communicates with the heart by means of its lateral branches, which anastomose in the various somites, sometimes on one side, sometimes on both, with branches of the lateral arteries. Capillary networks of great complexity are formed in the brain and in the ventral ganglia. A point of some interest is the unsymmetrical origin of the arteries

which supply the rostrum and the dorsal "Zoea"-spine of the larval carapace.

The blood from the respiratory appendages of the pleopods passes to the pericardium by a series of afferent canals in the abdomen.

Excretory System.—It is stated by Kowalevsky that the maxillary gland is well developed in the Stomatopoda, but no details as to its structure appear to have been published. A papilla on the posterior surface of the maxilla in *Squilla mantis* (Fig. 189, C, *o*) bears a minute terminal pore which may be the aperture of the duct of this gland.

Nervous System.—The oesophageal connectives are elongated, and a postoral antennal commissure is present. The first eight pairs of ganglia in the ventral chain are coalesced, but the remaining nine are widely separated.

Sense-Organs.—The paired eyes are always set on movable peduncles and vary greatly in size in the different species. The nauplius-eye, often present in the larvae, does not appear to have been found in the adult. Sensory filaments are developed on the outer branch of the external flagellum of the antennules.

Reproductive System.—The *testes* lie in the abdomen and have the form of fine convoluted tubes uniting posteriorly in an unpaired piece which lies in the telson and passing anteriorly into the vasa deferentia. Each vas deferens opens to the exterior at the end of a long penis springing from the inner side of the proximal segment of the last thoracic appendage, and differing from the corresponding organs of other Malacostraca not only in its great length but also in the fact that it is more or less strongly chitinised and is divided by a movable articulation about the middle of its length. In the posterior thoracic somites lie a pair of convoluted tubular glands which in their form and disposition have a remarkable similarity to the testes, being united anteriorly by a short unpaired piece and continued posteriorly into ducts which traverse the penes alongside of the vasa deferentia and open beside them at the tip. These glands and their ducts never contain spermatozoa and their function is unknown. The spermatozoa are spherical in form, without processes of any kind, and appear to be simple nucleated cells.

The *ovaries* are, in the mature female, very voluminous and closely approximated, so that they appear to form a single-lobed mass which extends through the abdomen and as far forward as the hinder limit of the carapace. In reality the two ovaries are only united, as is the case with the testes, by an unpaired portion lying in the telson. The oviducts open near the middle line on the sternal surface of the sixth thoracic somite, together with a small pocket-like invagination of the integument which functions as a receptaculum seminis. On the ventral surface of each of the three

last thoracic somites of the female lies a glandular mass, sending numerous fine ducts to the exterior. This is in all probability to be regarded as a cement-gland.

The eggs are of very small size, and are agglutinated together into a cake-like mass which either lies free in the burrow inhabited by the female or is carried by means of the last three pairs of chelate feet.

DEVELOPMENT.

Little is known of the embryonic development of the Stomatopoda, but their later history is extremely remarkable, on account of the prolonged larval life, the complicated metamorphosis, and the fact that the larval forms of the various species differ from each other more widely than do the adults. The later stages, which may reach a great size, form a conspicuous element of the pelagic fauna in the warmer seas, and many species were described by the older observers as adult animals under several generic names. It is very probable, as Hansen points out, that several forms of larvae belong to species and even genera which in their adult state are still to be discovered.

Two main types of larvae can be distinguished, corresponding to the old genera *Erichthus*, Latreille, and *Alima*, Leach, and the former can be further subdivided into a number of larval genera, *Gonerichthus*, *Lysioerichthus*, etc.

Though the earlier stages of all these are still very imperfectly known, it is certain that great differences exist between them as to the degree of development at the time of hatching. The longest series of larval stages appears to be passed through by certain *Erichthus*-forms, especially by those to which the names *Lysioerichthus* and *Coroniderichthus* have been given (larvae of *Lysiosquilla* and *Coronida*). In the youngest known stage of this series (Fig. 191, A) three regions of the body can be distinguished: (1) An unsegmented cephalic region bearing the median and paired eyes, antennules, antennae, mandibles, maxillulae, and maxillae, and giving rise to the great carapace which envelops the greater part of the body; (2) a thoracic region of eight somites, all of which are free from the carapace, the first five bearing biramous swimming-feet, while the last three are without appendages; (3) a broad tail-plate representing the still unsegmented abdomen. In the following stages the abdominal somites are successively segmented off in front of the tail-plate, which remains as the telson, and their appendages at the same time develop in regular order from before backwards, the uropods at first not differing from the appendages in front of them and not preceding them in order of development. The first and second thoracic limbs early lose their exopodites, and the second pair become greatly enlarged and assume their characteristic

form. The third, fourth, and fifth pairs undergo retrograde changes, losing their exopodites and remaining for some time as shapeless stumps, only later to resume their course of development into chelate limbs. It does not seem to be the case, however, as is sometimes stated, that they actually disappear. The last three

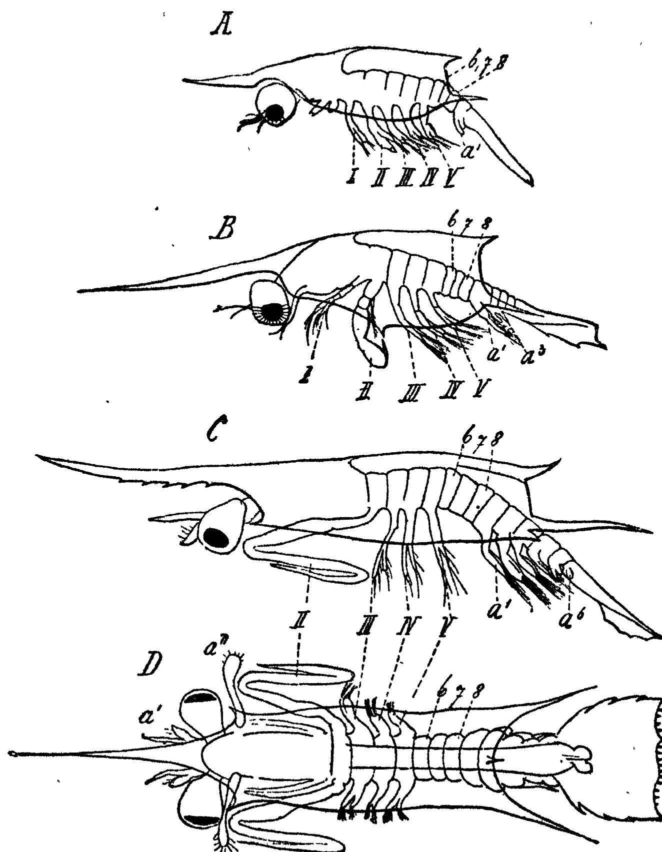


Fig. 191.

Consecutive stages of a larva of the first *Erichthus*-type. (According to Hansen, the larva represented in C and D belongs to a different species from those shown in A and B.) a', antennule; a'', antenna; a^1, first pleopod; a^6, uropod; I-V, first five thoracic appendages; 6-8, last three thoracic somites. (After Claus, from Korschelt and Heider's *Embryology*.)

thoracic somites remain for a long time devoid of appendages, and it is only at a late stage, when the appendages in front and behind are well developed, that rudiments of appendages begin to appear on them (Fig. 192). The adult form is only assumed after a considerable size has been reached, the carapace diminishing in size, becoming coalesced with the anterior thoracic somites, and

losing its spines, and the appendages gradually assuming their definitive characters. The development of the antennae appears to be peculiar in that the endopodite develops as a lateral branch, the distal portion of the larval appendage becoming the large exopod.

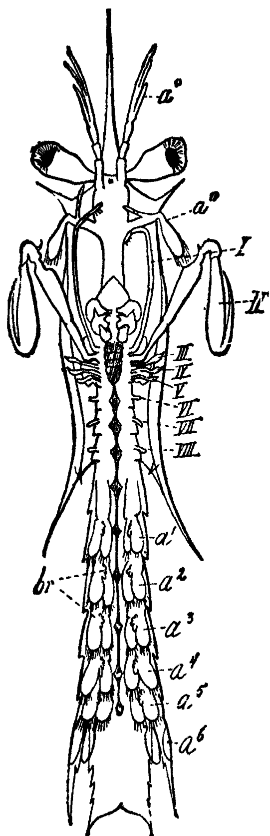


Fig. 192.

Later larva of the first *Erichthus*-type. a', antennule; a'', antenna; a^1-a^5, pleopods; a^6, uropods; *br*, rudiments of gills; I-VIII, thoracic appendages. (After Claus, from Korschelt and Heider's *Embryology*.)

In a second series of larval forms of the *Erichthus*-type (Fig. 193), belonging to the genera *Pseuderichthus*, *Gonerichthus*, etc. (*Pseudosquilla* and *Gonodactylus*), the youngest stage known possesses already four or five pairs of pleopods, and the last six thoracic somites are without any trace of appendages.

The larvae of the *Alima*-type (Fig. 194), belonging to the genus *Squilla*, are known to leave the egg at a stage corresponding with that last described. They are distinguished from all the preceding forms by the generally more slender body and short and broad carapace, and more constantly by differences in the armature of the telson and raptorial limbs.

Lister has described a very remarkable larva, which appears to correspond to a metanauplius-stage. The form of the carapace makes it very probable that it belongs to the Stomatopoda, and, if so, it shows that some members of the order leave the egg at a much earlier stage than has hitherto been supposed.

The great size attained by some of these larvae, especially by those of the *Alima*-type, which may exceed two and a half inches in length, has given rise to the suggestion that they are abnormally hypertrophied forms which, by being swept out to sea, have been prevented from completing their metamorphosis. As in the similar cases of the *Phyllosoma*-larvae among Decapods and the *Leptocephalus*-larvae of eels, however, there appear to be no grounds for accepting this view, and it is definitely rejected by Hansen as a result of his extensive studies on the group.

The metamorphosis of the Stomatopoda is of great importance in helping to interpret the larval forms of the Decapoda. While

the regular order of differentiation of the somites from before backwards is preserved, the retarded appearance of the posterior thoracic appendages shows the beginning of the process which has led to the suppression of these somites and appendages in the typical Zoea.

Notes on Habits, etc.

The Stomatopoda are exclusively marine, the adults generally inhabiting burrows in the sand or mud of the sea-bottom in shallow

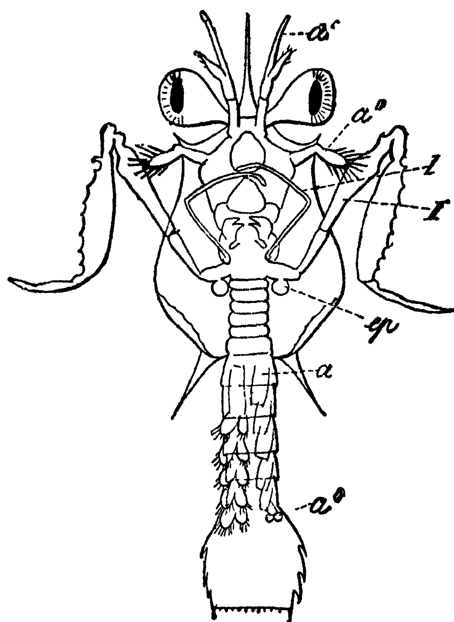


Fig. 193.

Larva of the second *Erichthus*-type (the *Pseuderichthus* group). a', antennule; a'', antenna; a, first pleopod; a^6, uropod; *ep*, epipodite; I, II, first two pairs of thoracic appendages. (After Claus, from Korschelt and Heider's *Embryology*.)

water (up to 180 fathoms), chiefly in the tropics, but extending north to Britain and Japan, and south as far as Auckland. Many species seem never to wander far from their burrows, into which they retreat with great rapidity when alarmed, and are thus seldom obtained by the ordinary methods of collecting. The larval stages, on the other hand, are exclusively pelagic, of glass-like transparency, and occur in great numbers in the plankton of the warmer seas. All the Stomatopoda appear to be of active, predatory habits. The range in size within the group is about from 38 to 340 mm.

Palaeontology.

The oldest undoubted Stomatopods are found in the Jurassic rocks of Solenhofen, and are referred to the genus *Sculda*, Münster, differing in many details from the living forms. Species referred to the genus *Squilla* occur in the Cretaceous deposits of Westphalia

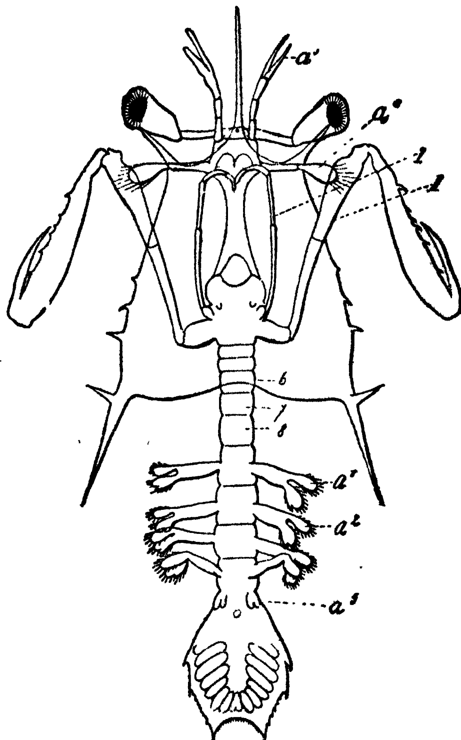


Fig. 194.

Young larva of the *Alima*-type. a', antennule; a'', antenna; a^1-a^5, pleopods; I, II, first and second thoracic limbs; 6-8, last three thoracic somites. (After Brooks, from Korschelt and Heider's *Embryology*.)

and the Lebanon, in which latter larvae of the *Erichthus*-type have also been recognised. Species of *Squilla* also occur in the London Clay and other Tertiary deposits.

Affinities and Classification.

Perhaps the most aberrant character of the Stomatopoda, and one which separates them not only from the other Malacostraca but from all other Crustacea, is the presence of distinct and

movable ophthalmic and antennular "somites." Whatever be the morphological value of these segments of the head, there can be no doubt that their separation in the Stomatopoda is a secondary and not a primitive character.

The movable rostral plate is a character of some interest from its resemblance to that of the Leptostraca; but it is to be noted that the spiniform rostrum of the larval Stomatopod is not articulated, while, on the other hand, the Decapod *Rhynchocinetes* shows the possibility of the ordinary rostrum becoming divided off by a movable joint from the carapace.

The lamellar epipodites of the first five pairs of thoracic limbs recall those of the Syncarida; the bifurcation of the outer flagellum of the antennules is only paralleled among the Caridean Decapods; the modification of the first pair of pleopods in the male may be compared with that found in the Euphausiacea and the Penaeid Decapods; the possession of an appendix interna on the pleopods is shared by the Leptostraca and the lower Eucarida. Other characters, such as the structure of the maxilla and the segmentation of the thoracic limbs, cannot be closely compared with those of any other Malacostraca. It seems most probable that the Stomatopoda are a lateral offshoot from the main stem of the Malacostraca, of which, in the absence of connecting links, it is as yet impossible to determine the exact relations.

The existing Stomatopoda form a very homogeneous group, within which only one family can be recognised, while many of the genera are separated by comparatively slight differences.

ORDER **Stomatopoda**, Latreille (1817).

Family SQUILLIDAE. *Squilla*, Fabricius (Fig. 186); *Lysiosquilla*, Dana; *Pseudosquilla*, Dana; *Gonodactylus*, Latreille; *Coronida*, Brooks.

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Note.—Page-numbers in thick type refer to the sections on classification.

THE END

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